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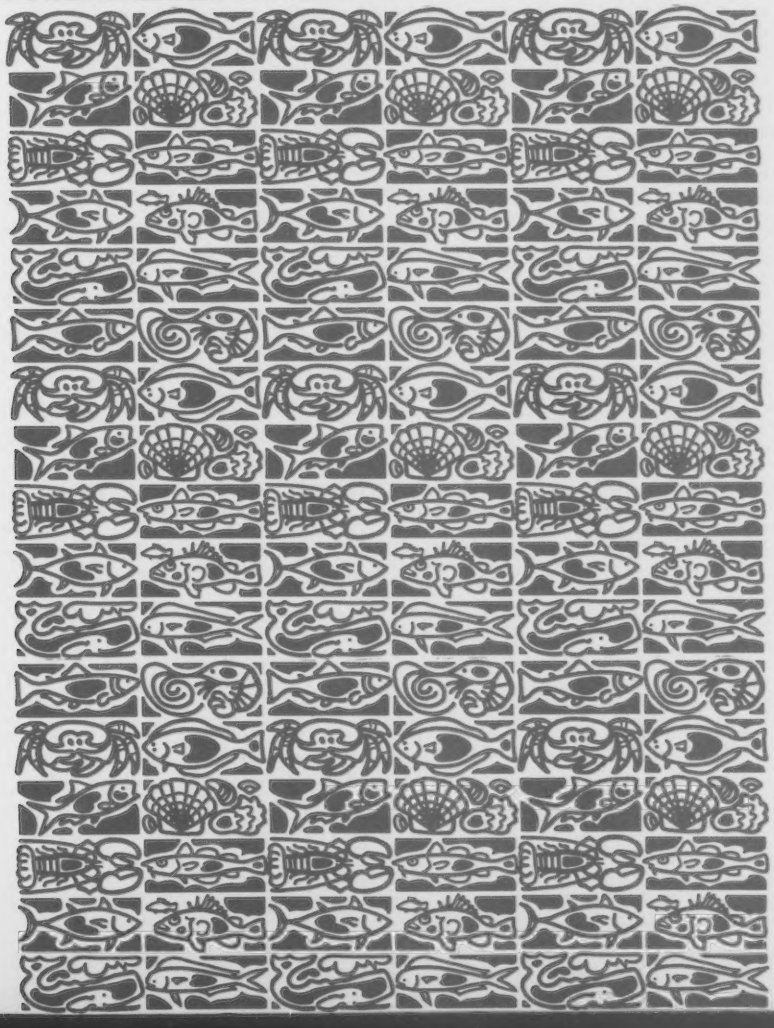
# Fishery Bulletin



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# Fishery Bulletin

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# Fishery Bulletin

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**Abstract.**–Nine lactating northern fur seals *Callorhinus ursinus* from St. Paul Island, Alaska, were instrumented with time-depth recorders and head-mounted radio transmitters in July and August 1985. Seven females were subsequently located at least once while at sea. Diving patterns obtained from females' time-depth recorders were then associated with their foraging locations. Generally two diving patterns were found; shallow-diving and deep-diving. The deep-diving pattern appears to be associated with feeding throughout the day over the continental shelf in water less than 200 m deep. The shallow-diving pattern is generally restricted to nighttime hours and probably occurs mostly over deep water. An analysis of the occurrence of food in stomachs of lactating fur seals collected in the eastern Bering Sea from 1958 to 1974 also suggests that seals collected over the continental shelf were more likely to be feeding during the day. We examine differences in the way shallow- and deep-diving females forage and discuss possible prey associated with the two diving patterns.

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# Diving Patterns and Foraging Locations of Female Northern Fur Seals

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The sexually dimorphic northern fur seal *Callorhinus ursinus* is a polygynous colonial breeder. Arrival of adult females and pupping are highly synchronous; most pupping occurs between 21 June and 31 July. Females give birth to a single pup within 1–2 days after arrival at the same site each year. Copulation occurs approximately 5 days after parturition, and females remain on shore 1–2 days more before going to sea to feed (Gentry and Holt 1986). The first feeding trip is the shortest, and subsequent trips gradually become longer (Gentry and Holt 1986). Periods of feeding at sea alternate with visits ashore to suckle their pups. The period from birth to weaning is approximately 125 days.

Compared with the land phase of the fur seal's life history, little is known of their life and behavior at sea. Kooyman et al. (1976) first reported on depth and duration of dives for a lactating northern fur seal. General patterns of diving behavior for breeding females were described by Gentry et al. (1986c). They found that individual females exhibit two discrete types of diving patterns: shallow and deep. Some females, exhibiting both patterns, showed the deep-diving pattern on the first and last days of a trip and the shallow pattern on other days. Fur seals exhibiting the deep-diving pattern typically dive to depths greater than 75 m without changing depth during a diving bout and dive at all hours of the day (Gentry et al. 1986c).

Feeding locations of individuals exhibiting different diving patterns, however, were unknown. Loughlin et al. (1987) initiated studies to determine what foraging areas in the Bering Sea were critical for lactating females. In 1984 using a ship, they located 11 females equipped with radio transmitters and tracked 4 of them to foraging locations. In 1985, they located 20 females with radio transmitters at sea from aircraft.

This paper reports our efforts to link fur seal diving behavior and foraging locations by instrumenting females with both radio transmitters (to determine location) and dive recorders (measuring depth of dive). We examine differences among females in diving behavior and their patterns of foraging, and discuss how diving behavior correlates with possible prey species.

## Study area and methods

This study was conducted at Zapadni Reef rookery on St. Paul Island, Pribilof Islands, Alaska, from 19 July to 16 August 1985 (Fig. 1). Nine female northern fur seals with pups were

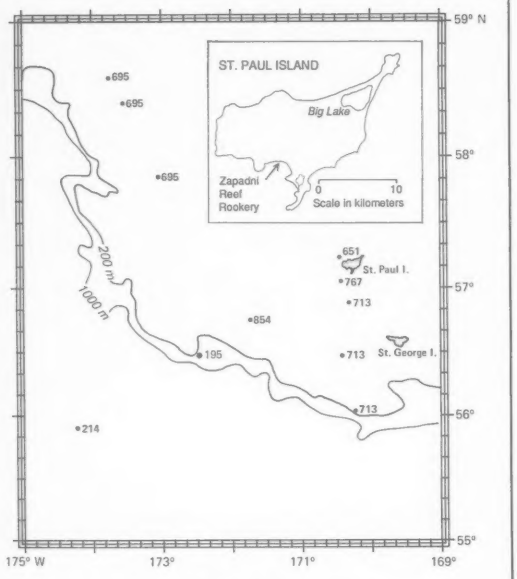


**Figure 1**

Study area with plotted locations of seven female northern fur seals equipped with time-depth recorders and their relation to the continental shelf break (the 200-m contour).

captured with a noose pole, removed from the rookery, and placed on a restraint board (Gentry and Holt 1982). Each female was tagged on the fore-flippers (Allflex sheep ear tag) and equipped with a radio transmitter (164 Mhz, Advanced Telemetry Systems, Isanti, MN) and a photomechanical time-depth recorder (TDR) (Meer Instruments, Solana Beach, CA). Radio transmitters were attached to the top of each seal's head with quick-setting epoxy resin (Devcon EK-40) (Loughlin et al. 1987) and TDRs were attached to seals by harness (Gentry and Kooyman 1986). After the epoxy resin had hardened (20–25 minutes), each female was returned to her capture site and released. Females were recaptured with a hoop net on their next visit ashore and the TDR was removed by cutting the harness. When possible, the mass for each female was determined at each capture.

Females were located at sea using a twin-engine airplane equipped with a two-element Yagi antenna mounted on each side of the fuselage (Loughlin et al. 1987). A total of 60 hours was flown on predetermined transects within 300 km of St. Paul Island at speeds of 100–120 knots and at 1200 m altitude.

Film from recovered TDRs was developed in either Agfa Rodinol or Kodak D-19. Each record was reproduced on paper with a 7× enlargement using copy flow xerography. At least three points of each dive were digitized on an electronic digitizing pad: the start, the end, and the maximum depth. These points allowed computation of dive duration, depth, and interdive surface interval. Each record was analyzed for bouts of diving using the same criteria used by Gentry et al. (1986c) for *Callorhinus*: five or more dives with less than a 40-minute surface interval between each dive.

The duration of diving bouts, number of dives per bout, percent time below the surface, and number of dives per hour were calculated as indices of the patterns of foraging.

The percent time spent below the surface was calculated separately for all dive bouts that occurred at mean depths of less than 75 m and for bouts greater than or equal to 75 m. An ANOVA on percent time below the surface was made after an arcsine transformation of the data. All comparisons for significant differences in depth were made using ANOVA with significance accepted at $\alpha \leq 0.05$.

The number of dives per hour was calculated for daytime (0700–2259) and nighttime (2300–0659) hours and for the entire record for each female. Percent of total dives for day and night hours was also calculated.

To further test the relationship between foraging locations and dive patterns, we used data from the National Marine Mammal Laboratory's pelagic fur seal database, which provided a large sample of lactating females that had been collected from July to September, 1958–74, from the eastern Bering Sea. We compared the proportion of stomachs with food to empty stomachs of lactating females collected over the continental shelf (<200 m depth) and for those collected off the continental shelf (>200 m depth; chi-square analysis). For the comparison, we used specimens obtained between the hours of 0600–1000 and 1400–1900 (we chose 0600 and 1900 because they were the start and the termination of sampling, and we arbitrarily selected 1000 and 1400).

## Results

Four of the nine females (nos. 195, 566, 651, 695) instrumented with TDRs and radio transmitters were deep divers, diving at all hours of the day; the other five (nos. 214, 308, 713, 767, 854) were shallow divers and dived primarily at night (Fig. 2).

Seven of these females, three deep divers and four shallow divers, were located at sea at least once. Female 195 was located on the third day of a 12-day trip at the continental shelf break. At this location the bathymetry changes rapidly, and because aerial locations are only approximate this female could have been

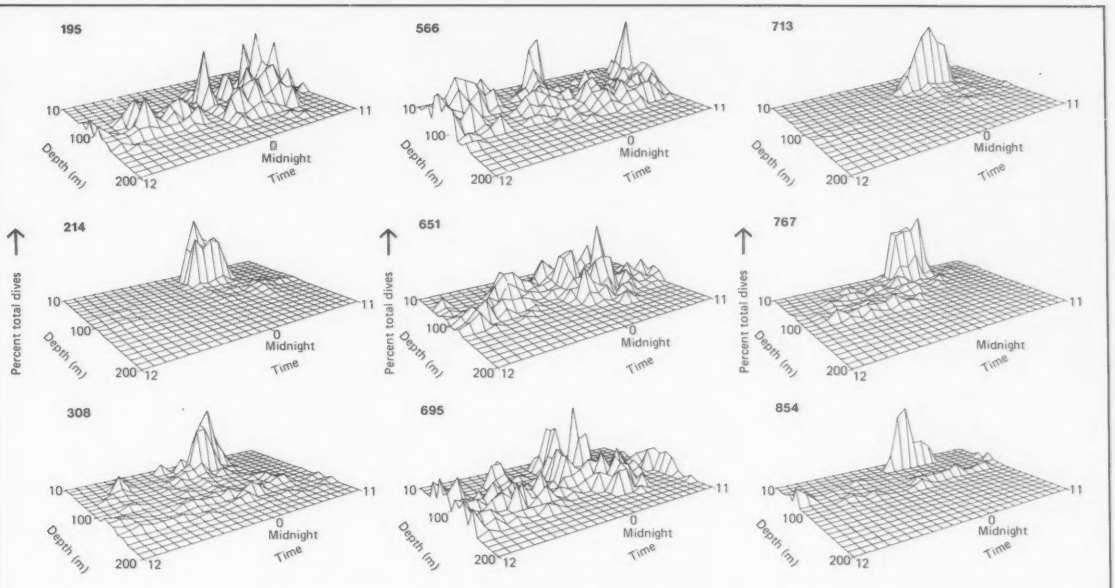


**Figure 2**

Three-dimensional plots of diving records for nine female northern fur seals at St. Paul Island, Alaska, in July and August 1985. Each plot represents the diving record (all dives ⩾20 m in depth) of one trip to sea for each female.

in water 140 m to 1400 m deep. On the day she was located, as well as on most days of her trip, she exhibited the deep-diving pattern. For a 24-hour period from 1200 on 4 August until 1200 on 5 August she made 70 dives (50% during the day) with a mean depth of 94.2 m (SD 18.5).

Two females (651 and 767) were located only once, on their return to St. Paul from a foraging trip (Fig. 1, Table 1). Female 651 was located 2.5 hours before she returned ashore and after she had completed 99% of her foraging trip. Her last dive was 6.9 hours before being located. Female 767 was located 8.2 hours before she returned ashore and 2.5 hours after her last dive.

Female 695 was located on three separate days, each time she was 110–160 km northwest of St. Paul Island, diving to depths greater than 100 m over the continental shelf in water 110–140 m deep. This female exhibited the deep-diving pattern every day of her 10-day trip, but also made seven dive bouts which had mean dive depths of less than 75 m, five of which occurred during the night.

Female 214 was located on the fifth day of a 12-day feeding trip in approximately 3500 m of water. On that day, as well as most other days, she exhibited the shallow diving pattern and dived primarily at night (Fig. 3).

Female 713 was also located on three consecutive days. She exhibited a foraging pattern of deep diving, day and night, on the first and last days of a foraging trip and shallow diving at night on other days. She was located on 25 July, the fifth day of a 7-day trip, 80 km south of St. Paul Island at the continental shelf break in approximately 200 m of water. On that day she dived exclusively at night with a mean depth of dive of 46.7 m (SD 17.1, $n$ 171). This was the night following her location at the shelf break. On the sixth day and on the last day of her trip she was located over the shelf and dived both during the day and night to much greater depths (mean depth of dive 101.3 m, SD 26.9, $n$ 67 for the sixth day, and 103.5 m, SD 11.0, $n$ 11 for the last day).

Female 854 was located on the first day of a 4-day trip over the continental shelf but within 18 km of the 200-m depth contour. From the time she left shore (2208) until she was located 20.8 hours later she had made 22 dives—all but three were greater than 75 m ($\bar{x}$ 75.6, SD 7.6). Of these dives, 77% were made before dawn. Her second night at sea was spent actively diving to depths of less than 35 m ($n$ 70, $\bar{x}$ 22.8, SD 19.6). She began diving at 2353 and dived continuously until 0340. This female was in transit across the continental shelf during the night, making occasional dives

**Table 1**

Mean depth (m) of dive for a 24-hour period (1200–1200) on the date of location for seven female northern fur seals equipped with radio transmitters and time-depth recorders, St. Paul Island, Alaska, 1985.

| Female ID | Date | Time | % time into trip | Depth of dive[1] | | | Nearest dive[2] | | Approximate depth at location |
|---|---|---|---|---|---|---|---|---|---|
| | | | | $\bar{x}$ | SD | $N$ | Depth | Time | |
| **Deep divers** | | | | | | | | | |
| 195 | 8/04 | 1411 | 21.7 | 94.2 | 18.5 | 70 | 70.5 | +1.63 | 140–1400 |
| 651 | 7/28 | 1613 | 99.0 | — | — | — | 71.5 | −7.10 | 50 |
| 695 | 7/28 | 1340 | 47.8 | 107.6 | 28.4 | 85 | 131.5 | −0.45 | 120 |
| | 7/29 | 1231 | 56.9 | 103.0 | 36.9 | 51 | 104.0 | +0.07 | 110 |
| | 7/30 | 1217 | 66.4 | 118.1 | 10.3 | 52 | 137.5 | −0.05 | 120 |
| **Shallow divers** | | | | | | | | | |
| 214 | 8/04 | 1313 | 39.0 | 35.5 | 20.9 | 159 | 85.6 | −1.57 | 3500 |
| 713 | 7/25 | 1758 | 69.7 | 46.7 | 17.1 | 171 | 60.6 | +6.35 | 200 |
| | 7/26 | 1414 | 80.9 | 101.3 | 26.9 | 67 | 89.5 | +7.40 | 110 |
| | 7/27 | 1717 | 96.1 | 103.5 | 11.0 | 11 | 99.5 | −1.47 | 80 |
| 767 | 7/26 | 1113 | 72.8 | — | — | — | 45.8 | −2.67 | 20 |
| 854 | 8/03 | 1855 | 23.1 | 39.3 | 18.2 | 78 | 71.5 | −1.23 | 120 |

[1]Females 767 and 651 had no dives during 1200–1200 on the date of location.
[2]Depth (m) of the dive closest to the time of location and the number of hours since the time of location.

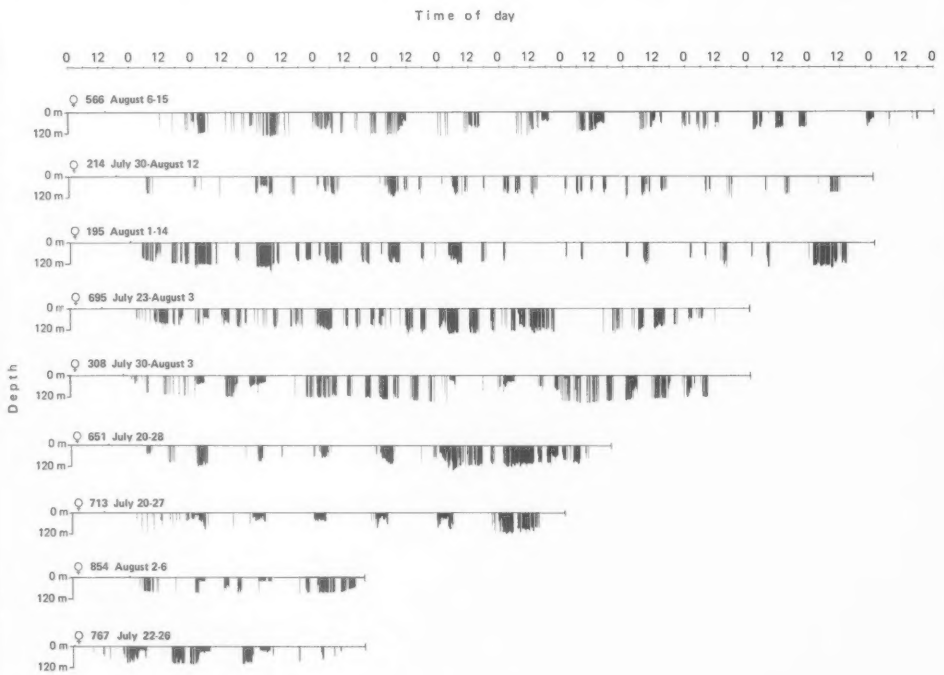


**Figure 3**

Two-dimensional plots of diving records for nine female northern fur seals at St. Paul Island, Alaska, in July and August 1985. Each plot represents the diving record (all dives ≥20 m in depth) of one trip to sea for each female.

**Table 2**

Record lengths, times to first and from last diving bouts, and mass of nine female northern fur seals instrumented with time-depth recorders in July and August 1985, St. Paul Island, Alaska.

| Female ID | Start | | Total hours | Time to first dive bout[1] | Time from last dive bout[2] | Mass (kg)[3] | | |
|---|---|---|---|---|---|---|---|---|
| | Date | Time | | | | 1 | 2 | Gain |
| **Deep divers** | | | | | | | | |
| 195 | 8/01 | 2308 | 290.22 | 4.72 | 12.25 | 34.0 | 37.6 | 3.6 |
| 566 | 8/06 | 1425 | 225.25 | 34.08 | 22.67 | 41.3 | 45.4 | 4.1 |
| 651 | 7/20 | 1442 | 196.33 | 14.72 | 12.75 | 31.3 | 33.6 | 2.3 |
| 695 | 7/23 | 1204 | 253.17 | 20.52 | 18.18 | 48.5 | 49.9 | 1.4 |
| **Shallow divers** | | | | | | | | |
| 214 | 7/30 | 1820 | 295.42 | 11.87 | 14.63 | 31.3 | 33.1 | 1.8 |
| 308 | 7/24 | 2042 | 242.50 | 2.98 | 15.13 | — | 39.5 | ? |
| 713 | 7/20 | 1342 | 178.28 | 23.03 | 8.12 | — | 34.0 | ? |
| 767 | 7/22 | 0041 | 114.75 | 18.98 | 18.73 | 39.5 | — | ? |
| 854 | 8/02 | 2208 | 91.01 | 4.65 | 3.00 | 40.1 | 40.4 | 0.3 |

[1]Time to first dive bout is the time from departure from shore until the first dive bout measured in hours. A dive bout is defined as any series of dives greater than five dives with surface intervals of less than 40 minutes (Gentry et al. 1986c).
[2]Time from the last dive bout (in hours) until the female returns to shore.
[3]Mass 1 is the mass taken upon deployment (the first capture), and mass 2 is the mass taken upon recapture (the second capture).

to depths greater than 75 m and then once near the shelf break, she began diving to shallow depths.

## Female mass and depth of dive

Seven of the nine females were weighed at instrument deployment, and eight were weighed when the instrument was recovered (Table 2). All females weighed twice showed a mass gain (range 0.3–4.1 kg). Time at sea ranged from 91 to 295 hours. Length of time at sea was not correlated with diving patterns or mass of the female ($r^2$ 0.0). No correlation was found between mass of individuals and their diving patterns ($r^2$ 0.0).

The mean maximum depth of dive for each deep diver was greater than 75 m whether considering day dives or night dives (Table 3). The mean maximum depth of dive for the shallow-diving females was less than 75 m (Table 3). When considering only night dives, shallow-diving females showed mean maximum depths of less than 50 m.

Two of the deep divers (195 and 651) showed no difference in depth of dives between day and night. The other seven females showed a significant difference in depth of dives between day and night. Six females dived deeper during the day than at night. The seventh (566) had significantly deeper dives at night than during the day (Table 3).

## Time from shore to the first dive bout and return

The time between departure from shore and the first dive bout was highly variable, as was the time between the last dive bout and the return to shore (Table 2). These times ranged from about 3 to 34 hours. Mean time to first dive bout was 15.06 hours (SD 10.26) and the mean time from last dive bout to shore was 13.94 hours (SD 5.88). There was no significant difference between the time to first dive bout and the time from the last dive bout (Mann-Whitney $P = 0.86$).

There were no differences in either the time to the first dive bout or the time from the last dive bout when comparing shallow divers with deep divers. The mean time to the first dive bout was 12.30 hours (SD 8.74) for shallow divers and 18.51 hours (SD 12.26) for deep divers (Mann-Whitney $P = 0.46$). The mean time from the last dive bout to shore for shallow divers was 11.92 hours (SD 6.29) and for deep divers was 16.46 hours (SD 4.93; Mann-Whitney $P = 0.54$).

## Foraging patterns

Deep divers showed a much lower percentage of dives at night than the shallow divers (Table 4). Females 566 and 695 made less than 50% of their dives at night. In general, shallow divers made greater than 70% of their dives at night (females 214 and 713 >90%) and deep divers less than 70%.

**Table 3**

Mean depth of dive for each dive record and for each record by day and night of nine female northern fur seals from St. Paul Island, Alaska, during July and August 1985.

| | Record total | | | Day hours | | | Night hours | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Female ID | Mean depth | SD | *N* | Mean depth | SD | *N* | Mean depth | SD | *N* | *P*-value[1] |
| **Deep divers** | | | | | | | | | | |
| 195 | 101.5 | 22.0 | 440 | 102.1 | 18.3 | 205 | 101.0 | 24.8 | 235 | 0.590 |
| 566 | 75.3 | 31.2 | 439 | 72.4 | 28.0 | 285 | 80.8 | 35.9 | 154 | 0.007 |
| 651 | 76.0 | 27.3 | 496 | 75.3 | 27.0 | 193 | 76.5 | 27.4 | 303 | 0.632 |
| 695 | 85.1 | 34.1 | 504 | 93.0 | 30.8 | 259 | 76.7 | 35.3 | 245 | 0.001 |
| **Shallow divers** | | | | | | | | | | |
| 214 | 38.7 | 23.1 | 1369 | 87.1 | 15.9 | 134 | 33.5 | 16.9 | 1235 | 0.001 |
| 308 | 60.6 | 42.1 | 832 | 94.8 | 41.6 | 230 | 47.5 | 34.3 | 602 | 0.001 |
| 713 | 45.4 | 21.7 | 900 | 85.1 | 25.4 | 55 | 42.8 | 18.7 | 845 | 0.001 |
| 767 | 33.3 | 27.7 | 431 | 72.9 | 22.6 | 90 | 22.8 | 17.6 | 341 | 0.001 |
| 854 | 40.6 | 28.2 | 312 | 63.6 | 15.2 | 80 | 32.6 | 27.3 | 232 | 0.001 |

[1] *P*-values are derived from a one-way ANOVA for differences in mean depth of dive between day and night hours.

**Table 4**

Total dives and dives/hour for day and night dives of nine female northern fur seals from St. Paul Island, Alaska, during July and August 1985.

| | | % total dives | | Dives/hour | | |
|---|---|---|---|---|---|---|
| Female ID | *N* dives | Day | Night | Total | Day | Night |
| **Deep divers** | | | | | | |
| 195 | 440 | 46.6 | 53.4 | 1.8 | 1.1 | 3.5 |
| 566 | 439 | 65.1 | 34.9 | 1.9 | 1.7 | 2.8 |
| 651 | 496 | 38.9 | 61.1 | 2.5 | 1.3 | 6.3 |
| 695 | 504 | 51.4 | 48.6 | 2.0 | 1.3 | 4.0 |
| **Shallow divers** | | | | | | |
| 214 | 1369 | 9.8 | 90.2 | 4.7 | 0.6 | 16.8 |
| 308 | 832 | 27.6 | 72.4 | 3.4 | 1.3 | 10.0 |
| 713 | 900 | 6.1 | 93.9 | 5.0 | 0.4 | 20.1 |
| 767 | 431 | 20.9 | 79.1 | 3.8 | 1.0 | 14.6 |
| 854 | 312 | 25.6 | 74.4 | 3.4 | 1.2 | 9.7 |

The number of dives/hour for the entire trip was greater for shallow divers than for deep divers (Mann-Whitney, $P = 0.02$). The maximum number of dives/hour for deep divers was 2.5 ($\bar{x}$ 2.0, SD 0.31), whereas the minimum number of dives/hour for shallow divers was 3.4 ($\bar{x}$ 4.1, SD 0.75). Although deep divers tended to execute more dives per hour at night than during the day, the difference was not significant (Mann-Whitney, $P = 0.11$). Shallow divers did, however, make more dives per hour at night than during the day (Mann-Whitney, $P = 0.02$). Regardless of which diving pattern females exhibited, they always made more dives per hour at night than during the day.

## Diving bouts

No differences in the total number of dive bouts per trip were detected between shallow and deep divers (Table 5). Although the number of dives that did not meet the dive-bout criteria tended to be greater for the deep divers, this difference was not significant (Mann-Whitney, $P = 0.07$). Differences in bout durations, number of dives per bout, and number of dives per hour within bouts were all greater for shallow divers (ANOVA, $P = 0.01$ for duration, $P = 0.01$ for dive number, $P = 0.02$ for dives/hour).

When all bouts were divided into those less than 75 m and those greater than or equal to 75 m, the percent of time spent below the surface was significantly different for shallow- and deep-diving bouts (ANOVA, $P = 0.01$). A greater percent of time was spent below the surface for shallow bouts (<75 m, $\bar{x}$ 0.35 hour, SD 0.11, $n$ 59) than for deep bouts (≥75 m, $\bar{x}$ 0.29 hour, SD 0.12, $n$ 102).

## Pelagic fur seal studies

During the hours 0600–1000, the stomachs of 740 postpartum females were sampled, 504 over the shelf and 236 off the shelf (Table 6). From 1400 to 1900 hours, 750 postpartum females were sampled, 513 over the shelf and 237 off the shelf.

Females collected in the morning hours off the continental shelf were more likely to have food in their

**Table 5**

Dive bout[1] statistics and effort within dive bouts for nine female northern fur seals, from St. Paul Island, Alaska, in July and August 1985.

| Female ID | Dive bouts | Dives excluded (%) | Bout duration (hours) | | | Dives per bout | | | Dives/hour in bout | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | $\bar{x}$ | SD | Max. | $\bar{x}$ | SD | Max. | $\bar{x}$ | SD | Max. |
| **Deep divers** | | | | | | | | | | | |
| 195 | 26 | 4.8 | 2.5 | 2.3 | 9.2 | 16 | 13 | 51 | 8.9 | 5.7 | 28.0 |
| 566 | 24 | 10.5 | 2.8 | 2.0 | 7.9 | 16 | 13 | 54 | 6.6 | 4.2 | 16.7 |
| 651 | 15 | 4.4 | 3.8 | 3.0 | 11.7 | 32 | 26 | 93 | 8.4 | 4.0 | 16.2 |
| 695 | 26 | 9.3 | 2.7 | 1.8 | 7.7 | 18 | 14 | 63 | 7.0 | 4.2 | 17.8 |
| **Shallow divers** | | | | | | | | | | | |
| 214 | 20 | 3.0 | 3.8 | 2.2 | 8.3 | 66 | 65 | 163 | 13.5 | 10.3 | 32.3 |
| 308 | 25 | 4.9 | 3.0 | 1.8 | 7.7 | 32 | 37 | 135 | 10.5 | 10.0 | 35.7 |
| 713 | 9 | 1.8 | 4.6 | 2.4 | 8.2 | 98 | 75 | 184 | 20.1 | 12.8 | 33.3 |
| 767 | 7 | 3.2 | 4.2 | 2.9 | 7.8 | 60 | 55 | 145 | 12.8 | 6.7 | 24.4 |
| 854 | 9 | 2.6 | 3.0 | 1.9 | 8.6 | 34 | 24 | 74 | 13.2 | 9.5 | 30.3 |

[1] A dive bout is defined as any series of dives greater than five dives with surface intervals of less than 40 minutes (Gentry et al. 1986c).

**Table 6**

The percent of stomachs with food of lactating northern fur seals collected over the continental shelf (in water <200 m deep) and off the continental shelf (>200 m deep). Collections were made from July through September, 1958–74.

| Time (hours) | Over the shelf | Off the shelf |
|---|---|---|
| 0600–1000 | 80.0 (403/504) | 95.3 (225/236) |
| 1400–1900 | 54.0 (277/513) | 39.7 (94/237) |

stomachs than females collected over the shelf (chi-square, $P<0.001$). Afternoon samples showed a reverse trend with a higher incidence of food in stomachs of seals collected on the shelf than off the shelf (chi-square, $P<0.001$).

## Discussion

### Dive patterns and foraging locations

The results of this study show that northern fur seal females diving in deep water beyond the continental shelf primarily exhibit the shallow-diving pattern and dive predominantly at night. Females feeding at or near the shelf break may exhibit both diving patterns. Females located on the continental shelf (which had not already completed their feeding trip) were more likely to exhibit the deep-diving pattern and dived to depths of greater than 75 m throughout the day and night. However, females found over the continental shelf had, at times, shallow dive bouts (<30 m) at night.

The pelagic fur seal database provided insight into the relationship between diving patterns and feeding locations of fur seals in the Bering Sea. If the deep-diving pattern is associated with feeding on the continental shelf, and deep divers feed during the day, one can test the hypothesis that females found over the continental shelf during the day have a greater probability of having food in their stomachs than those females found off the shelf, which would be diving predominantly at night. The analyses of the northern fur seal pelagic database support our finding that the deep-diving pattern is associated with the continental shelf by showing that females collected over the continental shelf were more likely to be feeding during the day.

### Dive patterns and probable prey

The feeding locations and dive patterns observed in this study are consistent with the known distribution of fur seal prey items. Kajimura (1984) summarized the variation in principal forage species for fur seals, depending on location. Fur seals feeding in the Bering Sea beyond the continental shelf over deep water fed on oceanic squid of the family Gonatidae (primarily *Gonatus* spp., *Berryteuthis magister*, and *Gonatopsis borealis*) or deep-sea smelts of the family Bathylagidae. These prey species, and fish with swim bladders, exhibit diel vertical migration and are at relatively shallow depths at night as they move vertically in synchrony with the deep scattering layer (Roper and Young 1975, Pearcy et al. 1977). It is during the night that they are fed upon by fur seals which rarely dive beyond 200 m (Gentry

et al. 1986b). Fur seals foraging over the shelf were likely to feed on walleye pollock *Theragra chalcogramma*, Pacific herring *Clupea harengus pallasi*, and capelin *Mallotus villosus* (Kajimura 1984). Each of these prey items is distributed throughout the water column over the shelf, depending on the sex and age of the individual and time of day; however, they are principally found near the bottom (Bakkala and Wakabayashi 1985). Even when prey are near the bottom over most of the shelf floor, they are shallower than the maximum diving depths observed for most fur seals and are accessible during all hours of the day.

The results of foraging effort for shallow and deep divers in this study are consistent with the results of Gentry et al. (1986c) in their study of diving of females from St. George Island. Costa and Gentry (1986) used isotopic turnover methods to measure food intake and metabolic rate in female fur seals instrumented with time-depth recorders. In that study of two deep-diving and two shallow-diving fur seals, the deep divers ate less food and expended less energy but gained similar body mass on a single trip to sea. Our results confirm their conclusion. In this study, using four measures—bout duration, dives per bout, dives per hour, and time spent below the surface—deep divers expended less effort on foraging than shallow divers. Deep divers apparently obtain greater energy per dive.

The difference in foraging effort of diving types may be explained by differences in energy content of prey, success rate for prey capture, and/or average size of prey captured. If success rate per dive and average size of prey were similar for both diving types, then energy content for the prey of deep divers would have to be greater. If prey were of similar size and energy content, then the prey of deep divers would have to be easier to capture. If success rate and energy content were similar, then the prey captured by deep divers would have to average a greater size per dive. Unfortunately, no data exist on success of individual dives.

Data on the energy content of prey items of northern fur seals suggest that Gonatus sp. and walleye pollock have similar energy content (M.A. Perez and T.R. Loughlin, NMFS Natl. Mar. Mammal Lab., Seattle, unpubl. data). No data exist for energy content of bathylagids. Perez and Bigg (1986) report on the size range of prey found in the stomachs of northern fur seals collected during 1958–74: walleye pollock, 4–40 cm (1721 prey from 71 stomachs); gonatid squid, 5–24 cm (>59 prey from 10 stomachs); deep-sea smelts, 8–12 cm (986 prey from six stomachs). The size range for Myctophiform fish prey and the mean size of prey were not reported.

## Transit times

The most frequently used measure of transit time, derived from time-depth records, has been the time from shore to the first diving bout and from the last dive bout to shore (Gentry and Kooyman 1986). Data from the current study show that female fur seals frequently feed while traveling to very distant feeding locations and that the time from shore to the first diving bout is only a subset of the total time in transit.

There was no difference in the time from shore to the first dive bout for the two types of diving patterns observed in this study. Similarly, the times from the last dive bout to arrival ashore were not different. Furthermore, no correlation was found between these times and feeding trip duration. It has been suggested, however, that a correlation exists between feeding trip duration and distance to feeding area (Gentry et al. 1986a). Gentry et al. (1986a) found that regressing transit time of individuals upon their trip duration resulted in a poor fit ($r^2$ 0.357). When they compared species averages using two tropical and two sub-polar otariid species, the correlation was much greater ($r^2$ 0.761). They concluded that transit time may largely determine trip duration for the species, but its effect is partly obscured by the large variation in transit times and trip duration of some individual animals.

The results of Loughlin et al. (1987) and of this study show that females feed while in transit to primary foraging areas. A correlation may exist between trip duration and total time spent in transit; however, measuring the time from shore to the first diving bout and from the last diving bout to shore is only a subset of actual time spent in transit and therefore an inadequate measure of total transit time. Without knowledge of either the swim velocity or the location of females (either through radio-tracking or with some instrument carried by the animal to record location) it is not possible to discern from a record of a time-depth recorder the actual time spent in transit.

## Classification of diving patterns

It is important to point out that any classification of diving patterns gives the impression that they are more discrete than they really are. It is more accurate to view any particular diving record as fitting into a continuum from strictly shallow diving at night to exclusively deep diving at all hours. The terminology used to categorize these diving patterns may overemphasize the importance of depth. It should be remembered that though deep- and shallow-divers are classified as such, the depth of dives may not be as important for identifying the pattern as the time of day in which diving occurs.

Before the advent of dive-recording instruments, one of the most important measurements used to assess changes in prey availability for pinnipeds and sea birds was the length of foraging trips. Foraging trips, however, may be useful only in documenting large-scale changes in prey availability (e.g., El Niño events). Dive-recorder instruments provide the opportunity to measure changes in the foraging environment on a finer scale. This work underscores the importance of quantifying dive patterns in elucidating differences in foraging strategies and in changes in the foraging environment.

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**Abstract.**– In Chesapeake Bay in June, the predatory lobate ctenophore *Mnemiopsis leidyi* and the eggs of the bay anchovy *Anchoa mitchilli* typically reach seasonal and localized abundance together. When examined at small vertical (1–3 m), horizontal (10–50 m), and temporal (6-hour) scales, the co-occurrence of *M. leidyi* and fish eggs (32.3–74.2% of which were *A. mitchilli*) was greatest in the northern reaches of the mouth of Chesapeake Bay, where the water column was well mixed, than in the southern reaches where the water column was stratified. Stratification to the south was effected by the Chesapeake Bay plume. With estimates of ctenophore clearance rate reported elsewhere and observed densities of ctenophores and fish eggs, potential predation was judged to be greatest in the northern reaches of the Bay mouth. The observation that co-occurrence and potential predation are greatest in areas where Chesapeake Bay water mixes with coastal shelf water implies that those fishes that spawn in low-salinity surface waters of well-stratified water columns may afford protection of their eggs from ctenophore predation.

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# Potential Predation on Fish Eggs by the Lobate Ctenophore *Mnemiopsis leidyi* Within and Outside the Chesapeake Bay Plume*

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Predation is probably the leading cause of mortality for fertilized fish eggs and yolksac larvae because starvation is not relevant for these early-life-history stages and because the short duration of egg incubation and yolk absorption for most teleosts limits transport to areas inimical to development (Bailey and Houde 1989). Assessments of the impact of predation on cohorts of fish eggs and larvae in the ocean, however, have been hindered by three problems: two practical, the third inferential. Eggs and larvae leave little identifiable residue in the guts of predators, and, as a result, direct estimates of the extent of predation are difficult. Predators and prey, moreover, are concentrated together in collecting devices, a situation that can result in artifically high feeding rates and inflated estimates of predation. Lastly, predation is often spuriously inferred from the inverse abundance of predators and prey, when presence and absence may actually reflect spatial and temporal segregation rather than removal of prey by predators. Such misinterpretations result from failure to consider the small-scale temporal and spatial distribution of predator and prey in differing water masses (Frank and Leggett 1982, 1985).

Among the known invertebrate predators of fish eggs and larvae, coelenterates and ctenophores are likely candidates for significant predation because of their high rates of ingestion and population growth (Alldredge 1984, Purcell 1985, Monteleone and Duguay 1988). Lobate ctenophores, in particular, are major predators of small zooplankton of limited mobility (Kremer 1979, Purcell 1985, Monteleone and Duguay 1988). They capture prey by pumping water past lobes lined with mucus and secondary tentacles (Larson 1988), a feeding mechanism that is seemingly well suited for the capture of fish eggs.

In Chesapeake Bay, a lobate ctenophore *Mnemiopsis leidyi* and the eggs of the bay anchovy *Anchoa mitchilli* reach seasonal and localized abundance together, thereby providing a predator and prey pair that is ideal for an evaluation of potential predation. *Mnemiopsis leidyi* is present from late fall through midsummer, and episodically explodes in abundance between May and July (Bishop 1967, Miller 1974, Kremer and Nixon 1976, Mountford 1980). *Mnemiopsis leidyi* can exhibit appreciable predation on fish eggs (*A.*

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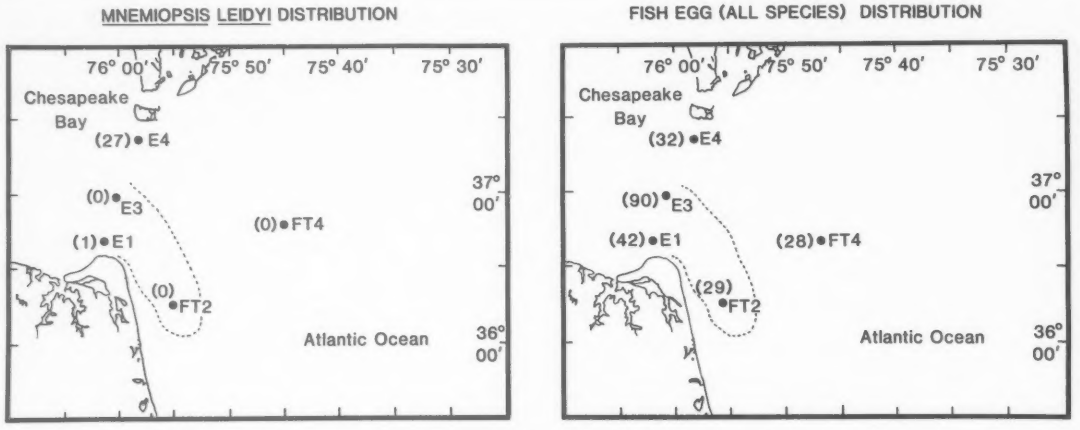


**Figure 1**

Positions of stations and mean station densities (numbers/$m^3$) of *Mnemiopsis leidyi* and fish eggs at the mouth of Chesapeake Bay. Dotted line indicates position of the Chesapeake Bay plume.

*mitchilli*) in the laboratory (Johnson 1987, Monteleone and Duguay 1988), but while it consumes some fish larvae in Chesapeake Bay (Burrell and Van Engel 1976), its predation on fish eggs in the field is not documented. *Anchoa mitchilli* spawns in the Bay in spring and summer and its eggs typically account for over 90% of all fish eggs present between May and August (Olney 1983).

The mouth of the Bay is characterized by water masses that differ spatially in both the vertical and horizontal dimensions (Boicourt et al. 1987) and provides hydrographic structure capable of shaping the spatial distribution of planktonic animals. Its complex hydrography is dominated by a buoyant plume characterized by a horizontal scale of 10–100 km, a vertical scale of 5–20 m, and a temporal scale of 1–10 days (Boicourt et al. 1987). As a result, the small-scale vertical and horizontal distributions of predator and prey can be observed synoptically in water columns of different structure within a confined study area.

Here we describe the small-scale spatial and temporal co-occurrence of *M. leidyi* and fish eggs at the mouth of Chesapeake Bay and assess potential predation.

## Methods

### Sampling protocol

Three stations were allocated across the mouth of Chesapeake Bay with two additional stations on the continental shelf (Fig. 1) such that some stations were within and others outside of the typical boundaries of the Chesapeake Bay plume (Boicourt et al. 1987). Each station was occupied for 30 hours between 11 and 21 June 1985 (the sampling period at station E1 was interrupted for 24 hours by vessel failure). At each station, hydrographic profiles (temperature, salinity, and specific gravity anomaly $\sigma_t$) and plankton collections at three nominal depths (surface, within the pycnocline, and below the pycnocline) were obtained once at four diel intervals (dawn, noon, dusk, and midnight). Fish eggs and ctenophores were collected with a 1-m Tucker trawl equipped with three 202-μm mesh nets, General Oceanic flow meters, and an Applied Microsystems Limited temperature, salinity, and depth recorder and towed at approximately 100 cm/second. Nets were opened at depth and fished along a horizontal trajectory for 30–60 seconds each; for subsurface strata, the trawl was lowered while the vessel was stopped and its nets were fished along a horizontal trajectory at depth. The trawl was positioned at nominal depth strata by the trigonometry of the warp angle and length. Triplicate samples were obtained at the surface; duplicate, discrete-depth samples were obtained within and below the pycnocline. With these sampling procedures, the trawl sampled on small vertical (1–3 m) and horizontal (10–50 m) scales.

All plankton collections were passed through a 6.4-mm mesh screen to separate ctenophores from ichthyoplankton. Ctenophores retained on this screen were fixed to prevent dissolution following the methods of Gosner (1971), then rinsed and preserved in 5%

formalin solution. Ichthyoplankton was preserved in either 5% formalin or 95% ethanol. All *M. leidyi* and fish eggs were counted except in those samples of exceptionally high ctenophore volume, where ctenophore number was estimated by volumetric subsampling and multiplication. Counts of ctenophores and fish eggs were averaged for replicate collections taken at a depth stratum and diel interval.

### Estimation of co-occurrence

Our intention was to assess the small-scale co-occurrence of ctenophores and eggs relative to the water masses overlying these stations and to then evaluate potential predation. Because the depth of each sample occasionally varied from the nominal and the trawl consequently fished through hydrographic discontinuities, some collections were omitted from consideration. Collections omitted were those in which salinity values, recorded during each 30–60 second fishing interval, varied outside a range of 1.5‰. This procedure eliminated seven of 35 collections at station E1 and none at E4, the two stations where ctenophores and fish eggs were consistently present and where we focused our assessment of potential predation.

### Estimates of potential predation

We estimated potential predation, for each depth and diel interval, as the product of clearance rate (the volume of water cleared of all prey per unit time per ctenophore), times the end points of the range of density of ctenophores (the number of ctenophores per unit volume, averaged for replicates), times the end points of the range in density of fish eggs (again averaged for replicates). A clearance rate of 168 L/day was used from Monteleone and Duguay (1988), who found that the clearance rate of fish eggs was independent of egg density (as well as the presence of alternate prey) and was positively and linearly related to experimental vessel size. This clearance rate was the highest rate observed for ctenophores 4.5–5.0 cm in length feeding in the largest vessels employed and falls roughly within the range of values reported elsewhere (Larson 1987). A sample of 10 preserved ctenophores from our collections averaged 8.5 mL in volume which converts to an average length of 4 cm (Kremer and Nixon 1976). We did not account for shrinkage.

## Results

### Distribution and co-occurrence

*Mnemiopsi leidyi* and fish eggs were consistently present only at stations E1 and E4 (Fig. 1). Pulses in densities of *M. leidyi* were evident, but did not conform to specific diel intervals or tidal phases (Figs. 2, 3). Egg density showed a diel pattern, with peak densities from dusk to dawn. Eggs of *Anchoa mitchilli* accounted for an average of 74.2% (range 23.0–98.5%) of the fish eggs at station E1 and 32.3% (range 0–62.9%) at E4.

*Mnemiopsis leidyi* and fish eggs were, for the most part, vertically segregated at station E1, but co-occurred, particularly in surface water, at E4. Vertical segregation at E1 (Fig. 2) reflected the physical stratification of the water column with a warm, low-salinity, surface-layer characteristic of the Chesapeake Bay plume overlying a cool, higher-salinity, bottom-layer characteristic of coastal shelf water (Boicourt et al. 1987). At E1, in the southern reaches of the mouth of the Bay, surface collections within the plume yielded higher egg densities, while subsurface collections yielded higher *M. leidyi* densities. Station E4, in the northern reaches and outside the plume, was unstratified with no thermo-, halo-, or pycnocline (Fig. 3). Water at this station apparently was a mixture of Chesapeake Bay water and coastal shelf water, likely the result of tidal, rather than wind, mixing. Winds, often responsible for mixing at the mouth of the Bay (Ruzecki 1981), were light to moderate during this sampling period (1–8 m/second).

### Potential predation

Overall, potential predation was greater in the unstratified northern reaches of the mouth of the Bay outside the plume (E4) than in the southern reaches stratified by the plume (E1), because of greater temporal and spatial co-occurrence of *M. leidyi* and fish eggs there. Range estimates of potential population predation were 0.1–14.7 eggs per $m^3$/day at E1, and 0–174.3 at E4 (Table 1).

## Discussion

The assessment of ichthyoplankton predation in the field has been based historically on the examination of predator gut contents or on the strength of a negative correlation of predator and prey densities, even though biases may result from the lability of fish eggs and larvae in the guts of predators, from the feeding of predators within the collecting device used to sample predator and prey (Purcell 1985), and from the spurious inference of cause and effect drawn from correlation analysis (Frank and Legget 1982, 1985). Few have resolved successfully the first two problems (Bailey and Houde 1989, Purcell 1989, Purcell and Grover 1990). In regard to the latter, the importance of small-scale spatial and temporal distribution of predator and prey

in evaluating predation is apparent across the mouth of Chesapeake Bay. Potential predation in the southern reaches where the Chesapeake Bay plume overlays coastal shelf water was low because of the relative lack of vertical co-occurrence there. In the northern reaches where the water column was well mixed, *M. leidyi* and fish eggs co-occurred in a more or less well-mixed water column, and as a result our estimates of potential predation were high.

The application of parameter estimates derived from laboratory predation experiments to the evaluation of the impact of gelatinous planktivores on their prey in nature, an approach that avoids field sampling errors, has other pitfalls (Purcell 1985). These problems relate to the unrealistic confines of experimental vessels, which constrain movement and small-scale hydrodynamics, and to unnaturally high experimental densities of predator and prey (Sullivan and Reeve 1982, de Lafontaine and Leggett 1988). The result is often artificially low estimates of clearance rate, values that are then used as functions in mathematical operations that range from simple multiplication of clearance rate and predator density (e.g., Reeve et al. 1978) to complex models that involve the swimming and foraging velocities and ambit geometries of motile predators and prey, and the turbulence of the environment in which they are embedded (e.g., Bailey and Batty 1983, Rothschild and Osborn 1988, Evans 1989). The simple approximation used herein was justified, in part, by the behavior of *M. leidyi* feeding on immobile fish eggs. Lobate ctenophores feed as a moving pump, pumping water continuously through mucus- and tentacle-lined lobes, while either swimming vertically or hovering (Larson 1988), and changing position in response to low prey density (Reeve et al. 1978). While the geometry of the predatory field of *M. leidyi* is unknown, we assume, given forage velocities of from 1–3 mm/second for its congener *M. mccradyi* (Larson 1987), that it encounters new water continuously. Although the gut capacity of lobate ctenophores is small, *M. leidyi* egests superfluous food in a mucus bolus when its gut is full and continues feeding; egested fish eggs, embedded in this bolus, are either dead or moribund (Johnson 1987).

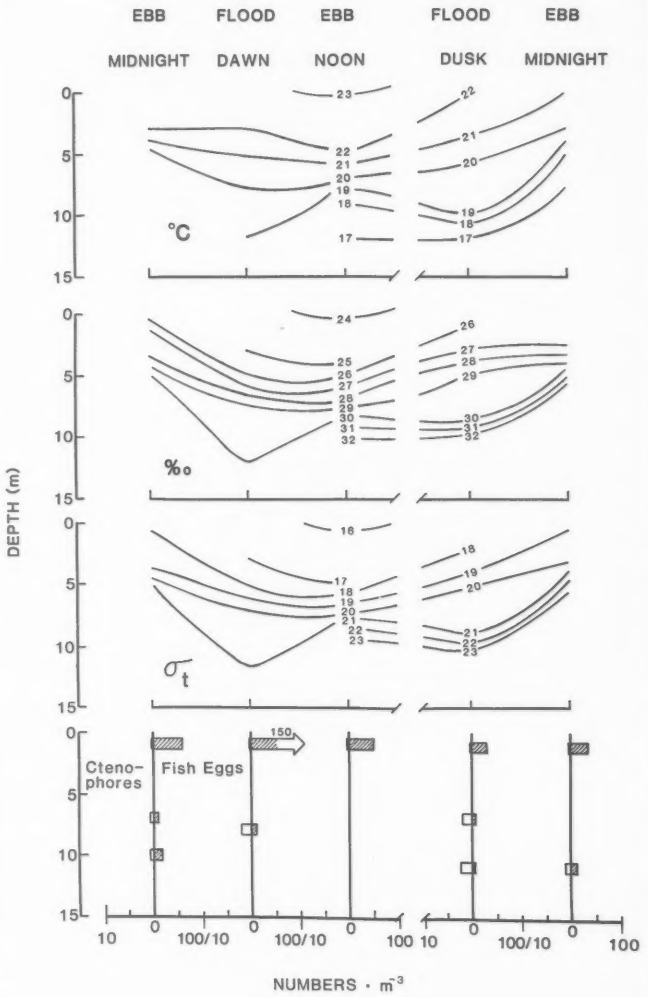


**Figure 2**

Temporal hydrographic sections (temperature, salinity, sigma-t) and densities (numbers/m$^3$) of *Mnemiopsis leidyi* and fish eggs at station E1 at the mouth of Chesapeake Bay. Vessel failure caused a 24-hour interruption in sampling between noon and dusk.

The observation that co-occurrence of *M. leidyi* and fish eggs, and consequently potential predation, is greatest in areas where Chesapeake Bay water mixes with coastal shelf water, coupled with the observation that *M. leidyi* are more abundant in regions of higher salinity within other estuaries, implies that those fishes

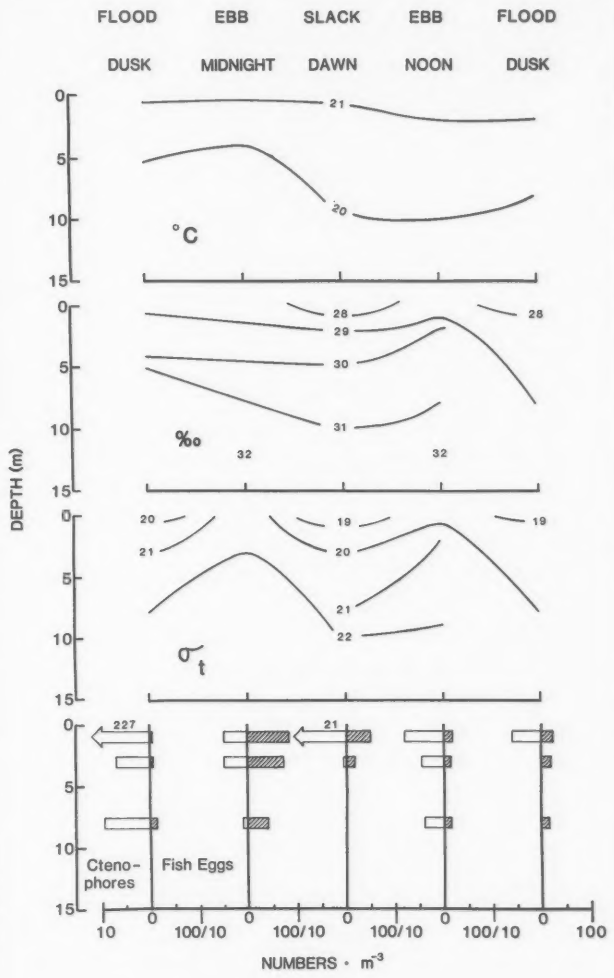


**Figure 3**

Temporal hydrographic sections (temperature, salinity, sigma-t) and densities (numbers/m$^3$) of *Mnemiopsis leidyi* and fish eggs at station E4 at the mouth of Chesapeake Bay.

**Table 1**

Potential predation of the lobate ctenophore *Mnemiopsis leidyi* on fish eggs at the mouth of Chesapeake Bay. Values are the end points of the range over five diel intervals.

| | Potential predation rate (eggs/m$^3$ × day) | |
|---|---|---|
| Strata | Station E1 | Station E4 |
| Surface | 0.1–14.7 | 21.0–174.3 |
| Pycnocline | 1.6–4.4 | 0–68.8 |
| Below pycnocline | 0.5–3.8 | 0–25.1 |

that spawn in low-salinity surface waters of well-stratified water columns may afford protection of their eggs from ctenophore predation. Estuaries typically fluctuate between stratified and unstratified conditions as a result of lunar periodicity and meteorological forcing. A survival advantage may be afforded by spawning in association with the predator free surface waters of the Chesapeake Bay plume.

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**Abstract.**–Spring ichthyoplankton surveys in the tidal freshwater reaches of Virginia rivers were used to document the temporal and spatial occurrence of spawning by striped bass *Morone saxatilis* (Walbaum). Single river systems were intensively surveyed in 1980 (York River system), 1981 (James River system), and 1982 (Rappahannock River). In spring 1983, all three river systems were sampled at approximately weekly intervals. Some spawning occurred in all years, including those yielding poor year-classes (1980 and 1981). Spawning occurred largely within the first 40 km of tidal freshwater in major rivers, except when drought conditions displaced spawning upstream in advance of encroaching saltwater. Eggs appeared in sharp, brief peaks of abundance, usually between the third week in April and the first week in May. Peak densities coincided with rapidly rising water temperatures in the range 13.7–19.5°C.

# Distribution of Striped Bass *Morone saxatilis* (Walbaum) Eggs and Larvae in Major Virginia Rivers*

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The importance of Chesapeake Bay spawning grounds to Atlantic coast stocks of striped bass *Morone saxatilis* (Walbaum) has long been recognized (Merriman 1941; Raney 1952; Briggs 1962; Alperin 1966; Schaefer 1967, 1968, 1972; Berggren and Lieberman 1978; Kohlenstein 1981; Fabrizio 1987a, 1987b). Striped bass spawning in Chesapeake Bay and its tributaries has been documented from collections of eggs and larvae (Tresselt 1952, Rinaldo 1971, Johnson and Koo 1975, Polgar et al. 1976, Conte et al. 1979, Kernehan et al. 1981, Setzler-Hamilton et al. 1981), and survey data on the distribution of juveniles or presence of ripe adults (Vladykov and Wallace 1952, Grant and Joseph 1969, Markle and Grant 1970, Grant 1974).

Direct documentation of striped bass spawning in Virginia rivers based on plankton collections of eggs and larvae was provided by consecutive single surveys of five rivers in April and May 1950 (Tresselt 1952); a single river survey during the entire 1966 spawning season (Rinaldo 1971); and a single river survey during the entire 1985 spawning season (McGovern and Olney 1988). This paper documents temporal and spatial occurrence of striped bass eggs and larvae in Virginia's major river systems. The York, James, and Rappahannock river systems, respectively, were surveyed in the years 1980–82; all three rivers were sampled in 1983.

## Methods and materials

Lower tidal freshwater portions of the James, Chickahominy, Pamunkey, Mattaponi, and Rappahannock Rivers were divided into 3-mile (5-km) strata, from which single stations were randomly selected prior to each sampling trip. Number of strata (in parentheses) and cruise dates were: the Pamunkey River (10), 16 April–13 June 1980 and 5 April–11 May 1983; Mattaponi River (6), 18 April–14 June 1980; James River (10), 22 April–19 June 1981 and 8 April–8 May 1983; Chickahominy River (7), 21 April–18 June 1981; and Rappahannock River (9), 5 April–6 June 1982 and 9 April–13 May 1983.

Stations were sampled semi-weekly to weekly within strata extending upstream from the limits of brackish water (~0.5‰) to beyond the observed occurrence of striped bass eggs. Collections at each station were stepped-oblique, daylight tows of a 60-cm bongo sampler, equipped with 333-μm mesh nets and flowmeters. Length of tows were 2–6 minutes; tows in deep water were of longer duration and tows encountering excessive detritus loads were shortened. Catches from the paired nets

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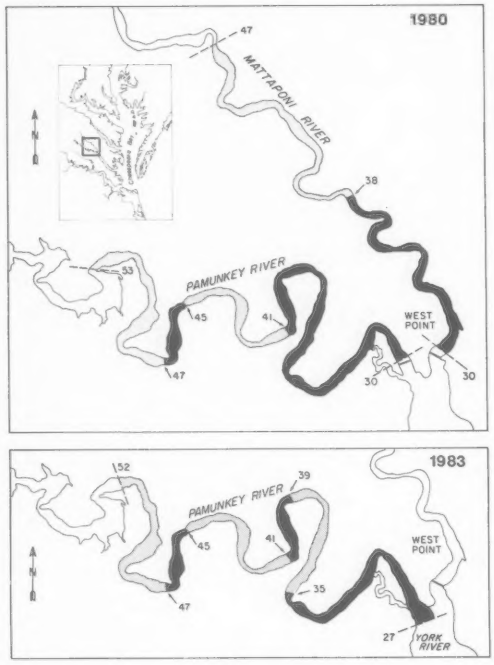


**Figure 1**
Spatial extent of observed striped bass egg occurrence, Pamunkey and Mattaponi rivers, 1980 and 1983. Over 80% of eggs occurred in solid black areas. Inset shows location in Chesapeake Bay region.

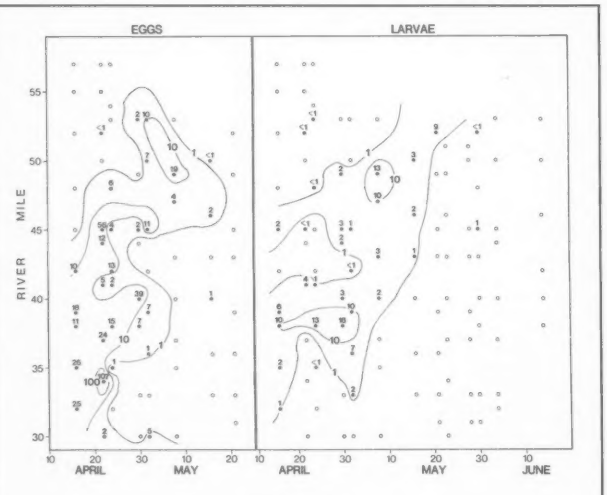


**Figure 2**
Spatial and temporal abundance (numbers/100 $m^3$) of striped bass eggs and larvae in the Pamunkey River, 1980. River miles are nautical miles above the York River mouth.

were combined and preserved in 5–8% buffered formalin. Sampling in 1983 was intended to document only egg occurrence; however, surveys on 4 and 11 May 1983 yielded some larval data. Surface and bottom measurements of temperature, salinity, and dissolved oxygen were made at each station.

Whole collections were sorted for striped bass eggs and *Morone* spp. larvae, except where large amounts of detritus necessitated examining only one-half of the collection. When bits and pieces of striped bass eggs were found, only intact eggs and separated embryos were counted. The area of peak spawning was defined as those strata that cumulatively contributed >80% of all eggs collected. *Morone* larvae lacking yolk material and larger than 8.5 mm standard length were cleared and stained for positive identification (Fritzsche and Johnson 1980, Olney et al. 1983).

## Results

### York River System, 1980 and 1983

Spawning extended approximately 40 km upstream from the limit of brackish water in the Pamunkey River in 1980 and 1983 and 27 km in the Mattaponi River in 1980. Peak spawning was recorded over 13 km on the Mattaponi River, while on the Pamunkey River it was observed in two disjunct regions (miles 27–41 and 45–47) in both years (Fig. 1). In 1980, eggs were found on initial surveys (April 16 and 18), indicating that spawning activity had already begun (Figs. 2, 3). Peak egg densities (>1/$m^3$) occurred on 22 and 25 April in the Pamunkey and Mattaponi rivers, respectively. In 1983 (Fig. 4), sampling on the Pamunkey River was initiated on 5 April, but few eggs were collected until 27 April, when peak densities for the season were encountered.

Abundance of larval striped bass was centered somewhat further upstream than eggs on the initial 1980 surveys, and all were yolksac larvae. Peaks in egg and larval abundance coincided more closely on subsequent sampling dates (Figs. 2, 3). Few larvae were collected after the 8 and 9 May surveys of the Pamunkey and Mattaponi rivers, none after 31 May.

Modal length of larvae in both rivers was 5 mm NL (notochord length) and most were yolksac larvae. All larvae captured after 16 May were 12 mm SL (standard length) or larger. In 1983, all larvae from the surveys of 4 and 11 May (the only collections examined for larvae) were yolksac larvae less than 6 mm in length.

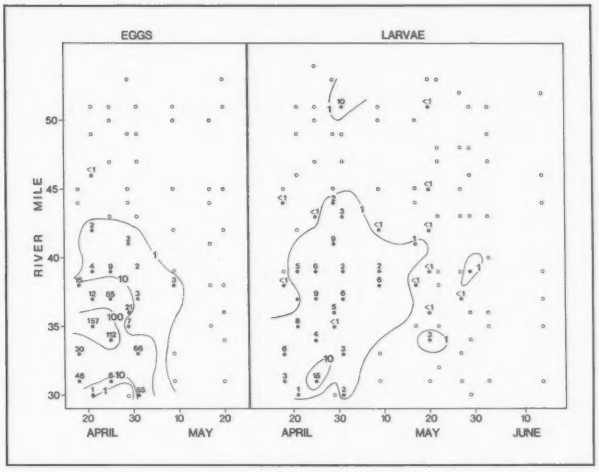


**Figure 3**
Spatial and temporal abundance (numbers/100 m$^3$) of striped bass eggs and larvae in the Mattaponi River, 1980. River miles are nautical miles above the York River mouth.

## James River System, 1981 and 1983

Location of peak spawning and maximum densities of eggs differed considerably between 1981 and 1983 (Fig. 5). Occurrence of eggs much farther upstream in 1981 was probably related to drought and intrusion of saltwater in winter and spring, 1980–81. Spawning extended over 35 km in 1981, and over 40 km in 1983. In both years

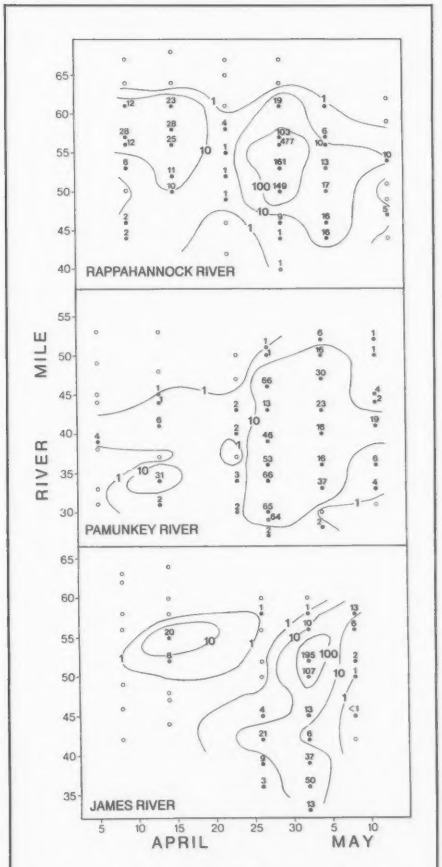


**Figure 4**
Spatial and temporal abundance (numbers/100 m$^3$) of striped bass eggs in three Virginia rivers, 1983. River miles are nautical miles.

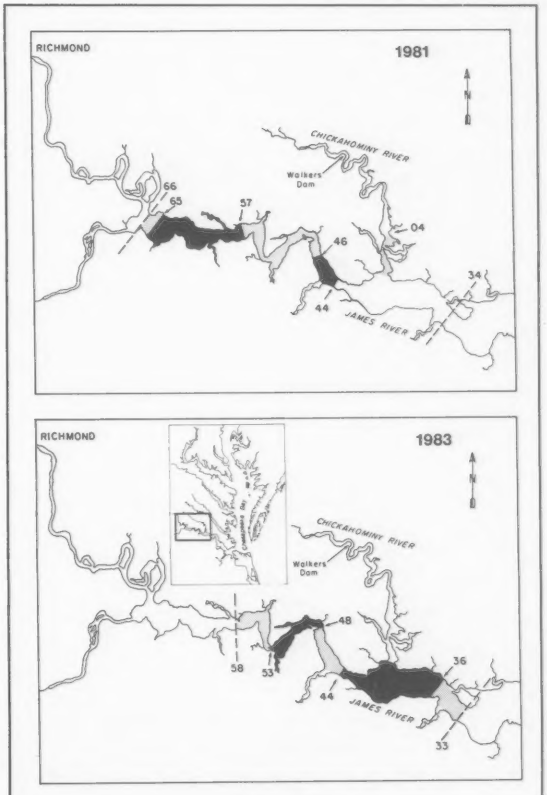


**Figure 5**
Spatial extent of observed striped bass egg occurrence, James River, 1981 and 1983. Over 80% of eggs occurred in solid black areas. Inset shows location in Chesapeake Bay region.

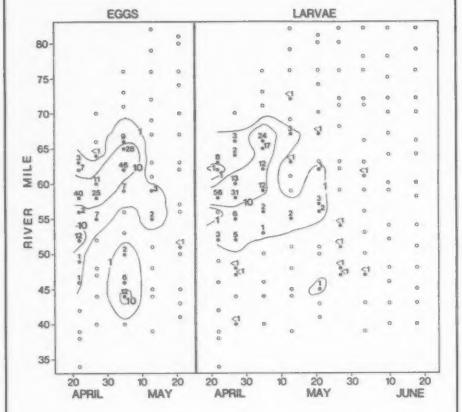


**Figure 6**

Spatial and temporal abundance (numbers/100 $m^3$) of striped bass eggs and larvae in the James River, 1981. River miles are nautical miles above the river mouth.

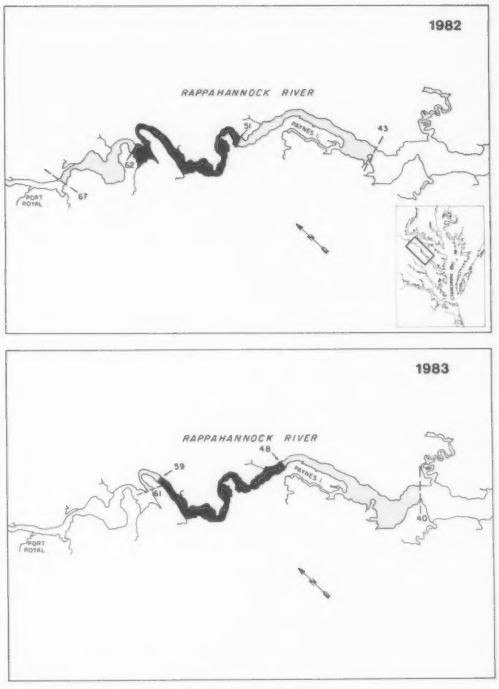


**Figure 7**

Spatial extent of observed striped bass egg occurrence, Rappahannock River, 1982 and 1983. Over 80% of eggs occurred in solid black areas. Inset shows location in Chesapeake Bay region.

peak spawning appeared to be bimodally distributed along the river channel. Eggs were present in both rivers on initial surveys of 1981 (21 April in the Chickahominy River and 22 April in the James River) in fresh to slightly brackish water and temperatures of 15.6–18.7°C. Maximum egg densities in the James River were only 46/100 $m^3$ in 1981 (13/100 $m^3$ in the Chickahominy), compared with 195/100 $m^3$ in 1983. These maxima occurred in both years during the first week in May, in tidal freshwater and similar temperatures (18.5–19.5°C), but at sites separated by 16 km (Fig. 6). In the Chickahominy River, eggs were restricted to the river's junction with the James and found on only two surveys, suggesting that eggs could have been spawned in the James River and tidally advected into the Chickahominy.

Larval striped bass were not present in collections from the Chickahominy River in 1981, and the river was not sampled in 1983. James River collections in 1981 yielded primarily yolksac larvae, found in maximum densities similar to those of eggs (Fig. 6). The modal length of larvae during the first 3 weeks of surveys in 1981 was 5.0–5.9 mm, but a few smaller larvae (4.0–4.9 mm) were hatched as late as 21–22 May. The maximum size of larvae increased from 7.0–7.9 mm in late April to over 13 mm on 4–5 June, the last survey in which striped bass larvae were captured. Only a dozen larvae larger than 9 mm were collected. In 1983, larvae from the early-May surveys attained densities of 31/100 $m^3$.

### Rappahannock River, 1982 and 1983

Eggs were found within the first 40 km of tidal freshwater in both 1982 and 1983 (Fig. 7). Peak spawning was observed between river miles 51 and 62 in 1982 and miles 48 and 59 in 1983. Eggs occurred in densities ranging between 1.4–330/100 $m^3$ during April 1982 and 0.7–50/100 $m^3$ in May of that year. None were found after the 11 May survey, and the maximum density occurred on 21 April in temperatures 15.7–16.6°C. In 1983, eggs were collected in all weekly surveys from 9 April to 13 May, but increasing densities were reversed by a cold snap in the third week of April, when only scattered eggs were found (water temperatures had declined from 13–14°C to 11–12°C). Egg densities peaked once water temperature rose in the last week of April, when a maximum of 477 eggs/100 $m^3$ was recorded. Eggs were rare by the final sampling date (May 13).

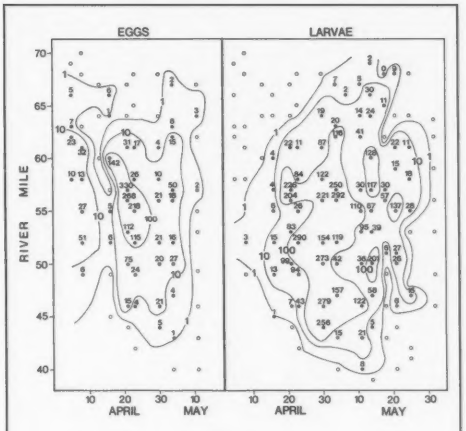


**Figure 8**

Spatial and temporal abundance (numbers/100 $m^3$) of striped bass eggs and larvae in the Rappahannock River, 1982. River miles are nautical miles above the river mouth.

Peak larval densities were recorded on the Rappahannock River in 1982 during late April and early May (Fig. 8). These densities were the highest observed in our 3-year study of Virginia rivers. Modal lengths of larvae were 5–6 mm NL until mid-May; all larvae from 21 May to the conclusion of sampling in June were at least 8 mm in length. In 1983, larvae from the early May surveys were all less than 8 mm in length and attained a maximum density of 103 larvae/100 $m^3$.

## Discussion

Tresselt (1952), Rinaldo (1971), McGovern and Olney (1988), and this study constitute the only direct observations on striped bass eggs and larvae in major Virginia rivers. Striped bass spawning in Virginia rivers occurred from early April through the first week or two in May 1980–83, and within the first 40 km of tidal freshwater, generally confirming earlier observations of Tresselt (1952) and Rinaldo (1971).

Tresselt (1952) observed spawning on the two major rivers of the York River system, the Pamunkey River (4–13 April 1950) and the Mattaponi River (13–30 April 1950). He found largest numbers of eggs 27 km above the mouth of the Pamunkey and 14 km above the mouth of the Mattaponi. Historic centers of successful spring fishing for striped bass were in these tidal freshwater rivers. Spawning in the Pamunkey River in 1966 occurred 8–48 km above West Point during 24 April–13 May 1966 (Rinaldo 1971). Surveys of Virginia striped bass spawning grounds in 1950 (Tresselt 1952) were inadvertently somewhat late in the Chickahominy and James rivers, but provide the only direct documentation of striped bass spawning prior to the present study. He found only three eggs in 30 collections in the Chickahominy River, 5–8 May 1950, and 57 eggs in 38 collections from the James River during 9–10 May. No direct observations on striped bass larvae were made prior to the present study. Use of the Rappahannock River as a spawning site by striped bass was also documented by Tresselt (1952), although his limited survey (four sampling dates in May 1950) yielded only five eggs.

Temporal occurrence of striped bass spawning is similar throughout Chesapeake Bay. In Virginia rivers, peaks in spawning were sharp and of limited duration. They occurred in the fourth week of April in York River tributaries in both surveyed years (1980 and 1983) and in the Rappahannock River in 1983; peak spawning was a week earlier in the Rappahannock River in 1982. Spawning in the James River was somewhat later, peaking in the first week of May in both 1981 and 1983. Peak spawning in this time-period is also typical for the Potomac River (Setzler-Hamilton et al. 1981) and in the upper Chesapeake Bay and Chesapeake and Delaware Canal (Johnson and Koo 1975, Kernehan et al. 1981). Although striped bass eggs were found in a wide range of temperatures (8.0–21.2°C), peak densities were limited to rapidly rising temperatures in the range 13.7–19.5°C and nearly always to freshwater. Annual differences in time of spawning within a given river system are most likely a result of differences in temperature and the rate of vernal warming.

Areas of peak spawning and the spatial extent of the spawn are remarkably similar among years and river systems, but differences can occur in years of drought. The present data from the James River contrasted a year of severe drought (1981) with one of near-average rainfall (1983). The estimated streamflow from the James River system into Chesapeake Bay during March, April, and May averaged only 69,000 cfs in 1981 compared with 180,000 cfs in 1983 (monthly summary reports of estimated streamflows entering Chesapeake Bay, 12/30/81 and 12/30/83, U.S. Geol. Surv., Towson, MD). Peak egg production was displaced 15 km upriver in 1981, in advance of encroaching saltwater, whereas interannual differences in location of peak spawning in the other river systems where drought was not a factor were insignificant (<2 km).

The tidal freshwaters of the Rappahannock River were surveyed for striped bass eggs and larvae in the spring of 1982, during production of what later was determined to be the strongest year-class measured in Virginia during the period 1971–82 (Colvocoresses

1989). The observed high density of eggs and larvae in 1982 and subsequent success of the 1982 year-class support the concept that attributes strong year-classes to exceptional survival of eggs and larvae on the spawning grounds, rather than absolute size of spawning stock (management actions designed to prevent overfishing and to increase size of spawning stock were not yet in effect). After 10 years of poor year-classes, i.e., 1972–81, the stock producing this 1982 year-class must necessarily have been small. Chapman's (1987, 1989, 1990) discovery of differences between genotype frequencies of 1982 year-class males and those of older Chesapeake Bay females is more direct evidence that strong year-classes can stem from successful spawning by relatively few females. Unfortunately, we have yet to determine which factors govern survival and growth of striped bass eggs and larvae on Chesapeake Bay spawning grounds, although recent research efforts are addressing this important question (e.g., McGovern and Olney 1988, Chesney 1989, Uphoff 1989).

## Acknowledgments

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**Abstract.**–Growth and mortality rates were compared for juvenile California halibut *Paralichthys californicus* from bay and open coast habitats. Growth was estimated by determination of size-at-age using daily increments in otoliths. No significant difference was observed in size-at-age for juvenile halibut between 6 and 41 mm from the bays and open coast. However, age-specific mortality rates estimated for halibut <70 days were highest for newly-settled halibut on the open coast. California halibut settled either in bays or on the open coast, but ultimately nearly all of the halibut that settled on the coast entered and used the bays as nursery areas during their first year of life or else they died. The advantages of bays as nursery areas may be a decrease in risk of mortality of newly-settled halibut and an increase in growth of larger juveniles that feed upon the abundant small fishes in the bays.

# Growth, Mortality, and Movements of Juvenile California Halibut *Paralichthys californicus* in Shallow Coastal and Bay Habitats of San Diego County, California

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The utilization of specialized nursery habitats by juvenile fish is a common phenomenon (Boehlert and Mundy 1988, Miller et al. 1986). Many of the fish species that utilize bays as nursery areas spawn in offshore waters, and move into bays as late larvae and early juveniles (Boehlert and Mundy 1988, Miller et al. 1986). The migration, location, and entry of larvae and juveniles into the bays involve complex behaviors that are particularly important on the Pacific coast of North America, where only 10–20% of the coastal habitat consists of estuaries and lagoons, compared with 80–90% on the Atlantic and Gulf coasts (Emery 1967). Possible consequences of the use of bays as nursery areas include faster growth because of high food production, warm temperatures, and decreased predation (Miller et al. 1986, Kneib 1987, Krygier and Pearcy 1986).

The California halibut *Paralichthys californicus* is a commercially important flatfish found in southern California coastal waters and bays (Frey 1971, Haaker 1975, Allen 1988, Love et al. 1986, Plummer et al. 1983). Eggs and larvae occur over the shelf and seaward, with greatest densities in waters less than 75 m deep and within 6 km of shore (Frey 1971, Gruber et al. 1982, Barnett et al. 1984, Lavenberg et al. 1986, Walker et al. 1987, Moser and Watson 1990). In past studies juvenile halibut rarely were taken on the open coast, suggesting that bays and lagoons might be the only significant nursery habitat (Plummer et al. 1983, Allen 1982, Kramer 1990).

The objective of this study was to determine the relative importance of bays as nursery areas and to evaluate the movements between bay and open coast habitats. To meet these objectives, I estimated habitat-specific distribution, abundance, and growth and mortality rates of juvenile halibut from both bay and open coast habitats.

## Materials and methods

### Distribution and abundance

California halibut were collected during a 2-year survey (September 1986–September 1988) of the open coast between Mission Bay and San Onofre, and two bays, Mission Bay and Agua Hedionda Lagoon (Fig. 1). A stratified random sampling design was used, consisting of four open coast blocks each with three depth strata (5–8 m, 9–11 m, and 12–14 m), and five blocks in Mission Bay and three blocks in Agua Hedionda Lagoon, each with three depth strata (0–1 m, 1–2 m, and 2–4 m) (Fig. 1).

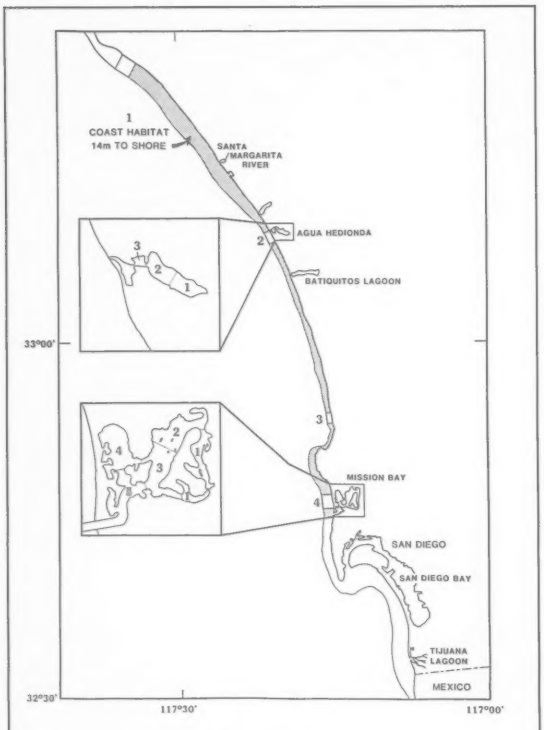


**Figure 1**

Location of sampling blocks. Open coast blocks are (1) San Onofre, (2) adjacent to Agua Hedionda Lagoon, (3) Torrey Pines, and (4) adjacent to Mission Bay. The two bays sampled are Agua Hedionda Lagoon and Mission Bay, with sampling blocks denoted.

For further description of the sampling design and the habitats see Kramer (1990).

Three gear types were used, all lined or made of 3-mm mesh: a 1.0-m wide beam trawl, a 1.6-m wide beam trawl, and a 1×6-m beach seine. The 1.6-m beam trawl, set from a 15-m research vessel, was used to sample the open coast and Mission Bay (Fig. 1). I sampled Agua Hedionda Lagoon and the areas of Mission Bay that were inaccessible to the larger vessel with the 1.0-m beam trawl, set from a 6-m skiff. The 1.0-m beam trawl and the beach seine were pulled along the bottom by two people to sample the shallow shoreline (<1m) in the bays. The trawls were fitted with a wheel and revolution counter to determine the distance traveled by the trawl along the bottom, allowing a quantitative assessment of fish density since the trawls had a fixed mouth opening (Krygier and Horton 1975). All trawls and seines were fished during the day.

**Table 1**

Gear weighting coefficients and their variances by length-class for conversion of shoreline collections by beach seine and 1-m beam trawl. Coefficients determined by 3-way ANOVA between gear types, blocks, and months of sample on density for each length-class. Correction terms are given for length-classes with significant gear effects ($P \leq 0.05$). There were no significant gear effects in the 1.0–1.6 m beam trawls for open water tows.

| Length class (SL, mm) | Correction term | Variance |
|---|---|---|
| 26–30 | 3.291 | 0.124 |
| 31–35 | 4.398 | 0.319 |
| 36–40 | 2.752 | 0.099 |
| 41–45 | 4.699 | 0.359 |

All flatfishes taken in trawls and seines were measured to standard length (SL) in mm. Density of halibut in 5-mm standard length-classes was determined for juveniles ⩽70 mm SL. The thirteen length-classes used were: SL⩽10 mm, 11–15 mm, 16–20 mm, continuing to 66–70 mm SL. Abundance was determined by multiplying the mean density for each habitat by the area of each habitat.

## Gear comparison

Densities based on the 1.0-m beam trawl collections did not differ significantly from those of the 1.6-m beam trawl for any length class (ANOVA, $P>0.05$, $n$ 826). However, the beach seine captured significantly fewer small halibut (26–45 mm SL) than the 1.0-m beam trawl (Table 1). Since significant biases existed, density and abundance estimates of halibut were corrected for the differences in gear efficiency by weighting the mean density and variance for each length class where significant differences in catchability were found (Table 1).

The weighted mean density for each gear type was calculated as

$$d_w = (d_1 + g d_2)/(1 + g)$$

where $d_1$ = unweighted density, $d_2$ = weighted density, and $g$ = weighting coefficient.

Estimated variance of the weighted mean $d_w$ was calculated as

$$V(d_w) = V(d_1) + g^2 V(d_2) + d_2^2 V(g) + V(g)V(d_2)$$

where $V(d_1)$ = variance of unweighted density, $V(d_2)$ = variance of weighted density, and $V(g)$ = variance of

weighting coefficient. Variance of the weighted mean was underestimated because the covariance terms were not included. Resampling techniques to estimate variance (e.g., bootstrap) were impractical because of the large size of the database.

### Age validation and determination

Laboratory-reared halibut larvae of known age were measured to standard length in mm and their sagittae excised and mounted in resin (Eukitt, O. Kindler, West Germany) on a microscope slide. Age was estimated using the methods of Methot (1981) and Butler (1987). A microcomputer interfaced to an electronic digitizer was used to measure and count increments on a projected image of the otolith from a high-resolution video camera mounted on a compound microscope. Increment counts of 45 larvae (3.1–9.1 mm SL) that were reared at 16–20°C in the laboratory were regressed against the known age of the larvae to establish a relationship between estimated and known age. Increments were formed daily: the slope of the relationship (0.969) did not differ significantly from unity ($P>0.05$). The regression of the number of increments on age of halibut larvae (5–29 days) was

$$\text{Age (days)} = 3.496 + 0.969 \times (\text{no. increments})$$

where $r^2 = 0.981$, SE constant = 1.055, SE slope = 0.018, and range of increment counts = 1–26) (Fig. 2). Daily formation of rings has also been found in juveniles 30–70 mm SL (Kicklighter 1990). The first increment is deposited about 3.5 days after hatching, coinciding with the day of first feeding (Gadomski and Peterson 1988). I added 3.5 to the number of increments counted on the otolith so that age was equivalent to the number of days from hatching.

### Ageing of field-caught halibut

Juvenile halibut from field collections were measured alive and either frozen or preserved in 80% ethanol. Sagittae were dissected and increments counted using the techniques described above. Sagittae from juveniles >20 mm SL were polished with 400- and 600-grit wet sandpaper before counting.

A total of 120 field-caught halibut were aged: 50 from Mission Bay, 19 from Agua Hedionda Lagoon, and 51 from the open coast. Larval sagittae are symmetrical and nearly circular (Fig. 3A), but after metamorphosis additional foci develop and the sagittae became asymmetrical, with maxiumum deposition along the rostral axis (Karakiri et al. 1989) (Fig. 3B). This shift in the axis of sagittal growth produces areas

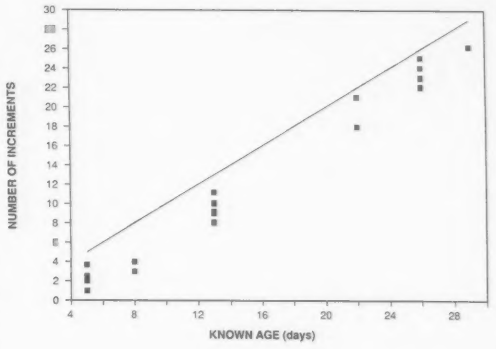


**Figure 2**
Age validation of California halibut sagittae. Number of increments counted on the sagittae are compared with the known age of laboratory-reared larval halibut ($n$ 45). Straight line represents a one-to-one relationship of increment number and known age.

that are difficult to interpret (Fig. 3). These areas correspond to a period of about 7 days after metamorphosis. I estimated the number of increments in regions of transition between foci by counting the number of increments that occurred in an adjacent area on a different axis (Fig. 3). The relationship between standard length (mm) and otolith radius (μm) was linear for halibut >10 mm SL (Fig. 4).

### Mortality estimates

I did not use data from the 1987 survey for estimating mortality because nearly all of the 1987 year-class occurred in bays and comparisons of mortality between bay and coast habitats were an essential step in the analysis. The relationship between abundance and age (estimated from the length-at-age relationship) of the 1988 year-class was used to estimate age-specific mortality rates.

I used seven different models to estimate age-specific instantaneous mortality rates. Three of the models were estimates based on the following assumptions regarding the relationship between survival rates and age (Barlow 1982): (1) Age-specific survival rates increase linearly with age; (2) age-specific survival rates increase exponentially with age; and (3) age-specific survival rates approach an asymptote with age. The two daily production models estimated age-specific instantaneous mortality rates based on the relationship between daily production (abundance of length class/duration of length class) and age (Lo 1985). The last

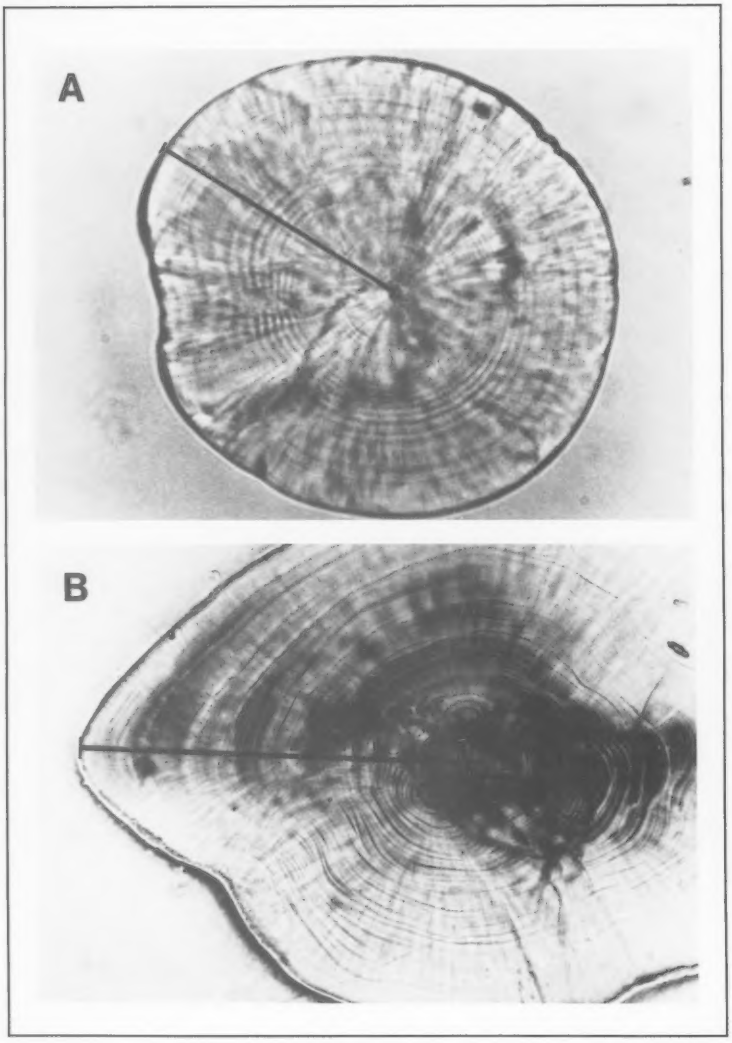


**Figure 3**
Photomicrographs of California halibut otoliths. (A) Sagitta from halibut 6.94 mm SL, estimated age 22 days. Distance of drawn radius, 70 μm. (B) Sagitta from halibut 48 mm SL, estimated age 109 days. Distance of drawn radius, 890 μm.

two models were simple linear estimates, using a linear regression of ln-transformed abundance-at-age on age (constant mortality rate with age) and on ln(age) (age-specific mortality rates). The sum of squared deviations of observed abundance-at-age from the calculated or transformed abundance-at-age predicted by each model was used to determine the model that best fit the data.

Mortality estimates for halibut from the open coast include loss of juveniles from the open coast population due to emigration into the bays. These estimates are used to calculate age-specific emigration rates by comparing the apparent mortality (= mortality + emigration) on the open coast to the total mortality calculated for the population on the open coast and in the bays.

## Results

### Effects of season and location on size-at-age

Relationships between halibut length and age did not vary significantly between seasons or between habitats. Analysis of covariance indicated no significant difference in length-at-age between fish that had birthdates in the spring and those with birthdates in the late summer and fall, but the sample size was small for fall fish ($n$ 9) (Table 2). The common slope was 0.6206 (SE 0.0905).

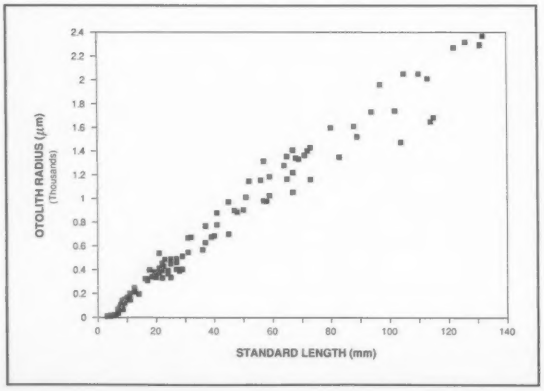


**Figure 4**
Relationship between otolith radius (μm) and standard length (mm) of California halibut ($n$ 120).

Analysis of covariance also indicated no significant difference between juveniles from the bays and the open coast in the relationship between length and age (Table 2). The comparison was made between fish from the bays and the open coast. The common slope was 0.471 (SE 0.0238). Therefore, I used the pooled data for all estimates of growth ($n$ 120).

**Table 2**

Regression analysis and analysis of covariance (ANCOVA) of size-at-age by season and by habitat. Slopes and intercepts were compared using ANCOVA; all tests were not significant at $P>0.05$.

| Covariates | $N$ | Size range (mm) | Equality of | | $F$-statistic | |
|---|---|---|---|---|---|---|
| | | | Intercept | Slope | Intercept | Slope |
| **Seasons** | | | | | | |
| Spring | 26 | 27–80 | −7.6 | 0.637 | 1.68 | 0.051 |
| Fall | 9 | 27–83 | −8.6 | 0.594 | | |
| **Habitats** | | | | | | |
| Coast | 51 | 6.8–41 | −7.2 | 0.468 | 3.87 | 0.035 |
| Bays | 26 | 8.3–41 | −4.7 | 0.478 | | |

## Length-at-age

The relationship between standard length (mm) and age (days) was best described with the Gompertz growth function,

$$\text{Length} = P_1 \times \exp(P_2(1 - \exp(-P_3 \times \text{age})))$$

with $P_1 = 2.13$, $P_2 = 4.77$, and $P_3 = 0.011$, and an estimated mean square error of 0.99 ($2SE_{P_1} = 0.34$, $2SE_{P_2} = 0.137$, $2SE_{P_3} = 0.0013$) (Fig. 5A). The parameter $P_1$ closely estimates the length-at-hatching, which is 2.0 for halibut (Ahlstrom et al. 1984).

The relationship of age-at-length was determined with the function,

$$\text{Age} = -88.347 \times \ln(\ln(\text{standard length} \times 251.07)/-4.769)$$

derived from the Gompertz relationship for size-at-age (Methot 1981) (Fig. 5B). The variance in the estimate of age-at-length increases with increasing length; the 95% confidence interval (CI) for a halibut age 25 days is ± 6 days, but for a 90-day-old halibut the 95% CI is ± 19 days (Fig. 5). This relationship was used to convert length-classes into age-classes using the mean of each length-class (Lo 1985).

I used the method outlined by Methot (1981, equations 1–5) to compute the age-specific daily growth rates. Length-specific daily rate of growth and the variability in growth rate increased with increasing length: the slowest growth occurred just after transformation (SL 6–10 mm), with daily growth <0.3 mm/day, and maximum growth rates of about 1 mm/day occurred in juveniles 70–120 mm SL (between 110 and 160 days) (Fig. 6). These growth rates are similar to those measured by Allen (1988) who estimated that juveniles 21–29 mm SL grew at 0.36 mm/day, and juveniles 19–47 mm SL grew at 0.99 mm/day.

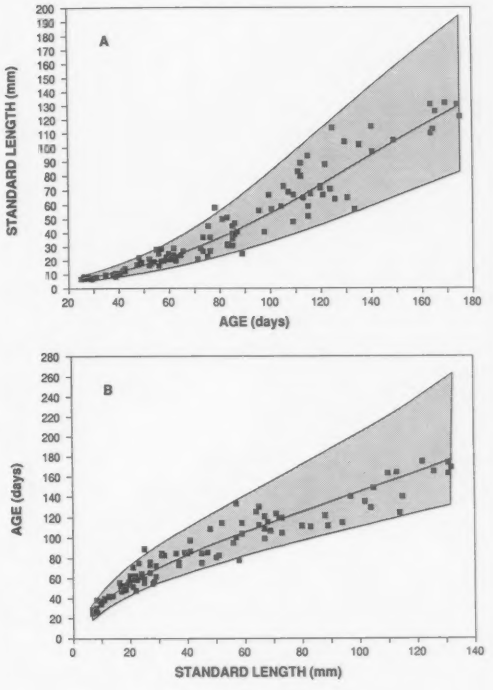


**Figure 5**

Gompertz relationship with 95% confidence intervals fitted to length-at-age of California halibut. (A) Standard length-at-age; (B) estimated age-at-length (mm).

## Distribution and abundance

Juvenile California halibut 16–70 mm SL were present in the bays during January–July 1987 and March–September 1988, and on the open coast between May and September 1988. The distribution of transforming larvae and juveniles on the open coast differed for the 1987 and 1988 year-classes, with very few larvae and no small juveniles taken on the open coast in 1987,

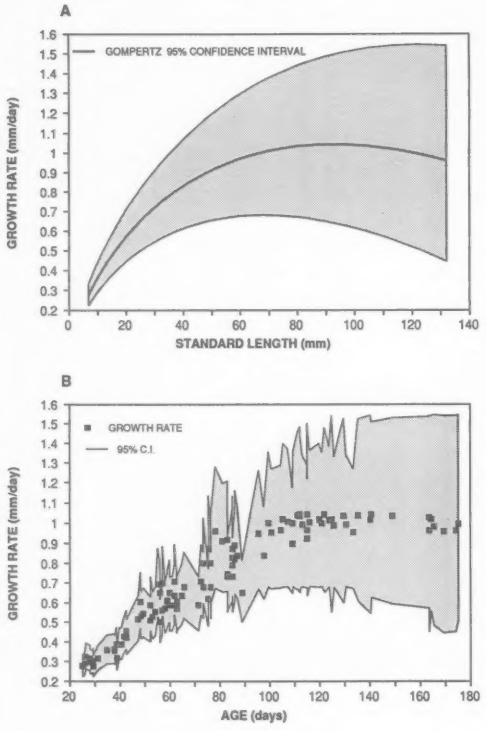


**Figure 6**

Growth rates of juvenile California halibut estimated from the Gompertz parameters for length-at-age, shown with 95% confidence intervals. (A) Relationship between growth rate (mm/day) and length (mm); (B) relationship between growth rate (mm/day) and age (days).

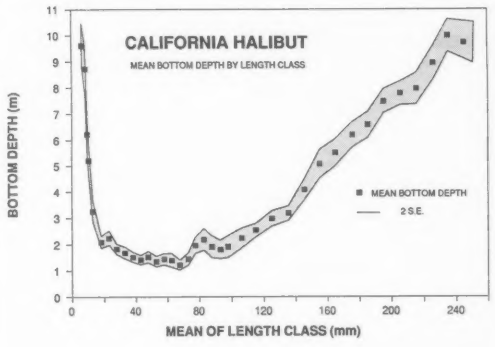


**Figure 7**

Mean depth of capture of California halibut by standard length-class (mm). Length-classes (mm) were ⩽7 (*n* 54), 8 (52), 9 (47), 10 (38), 11–15 (116), 16–20 (198), 21–25 (161), 26–30 (161), 31–35 (116), 36–40 (116), 41–45 (138), 46–50 (127), 51–55 (124), 56–60 (92), 61–65 (81), 66–70 (92), 71–75 (74), 76–80 (45), 81–85 (53), 86–90 (50), 91–95 (42), 96–100 (53), 101–110 (74), 111–120 (103), 121–130 (101), 131–140 (154), 141–150 (154), 151–160 (109), 161–170 (129), 171–180 (143), 181–190 (121), 191–200 (135), 201–210 (128), 211–220 (88), 221–230 (73), 231–240 (60), and 241–250 (47).

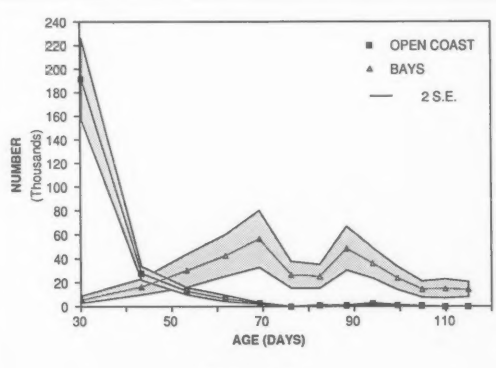


**Figure 8**

Abundance of juvenile California halibut by age-class for open coast and bay habitats in 1988.

whereas transforming larvae and newly-settled juveniles were common in 1988. Only the 1988 year-class was used to compare growth and mortality rates for juvenile halibut in bays and on the open coast. Further information on the distribution patterns of juvenile California halibut can be found in Kramer (1990).

The length distribution of transforming larval and juvenile halibut varied with depth. The smallest length-class of halibut (⩽7 mm SL) was taken at an average depth of 9.6 m (SD 3.08, *N* 54). The mean depth of occurrence decreased with increasing length up to a mean length of 67.8 mm SL (Fig. 7). At this size, the trend reversed, with mean depth of occurrence increasing with increasing length (Fig. 7). This pattern of length-at-depth indicates that transforming and newly-settled halibut move into shallower water along the open coast and into the bays, and halibut >70 mm SL move into deeper water habitats within the bays (maximum bay depths were <5 m) and eventually move out of the bays to the open coast (Fig. 7) (Plummer et al. 1983).

The age of peak abundance of juvenile halibut in the bays in 1988 was equivalent to the average time required for newly-hatched larvae to move from the continental shelf to the bays. Peak abundance was at about 70 days in both Mission Bay and Agua Hedionda

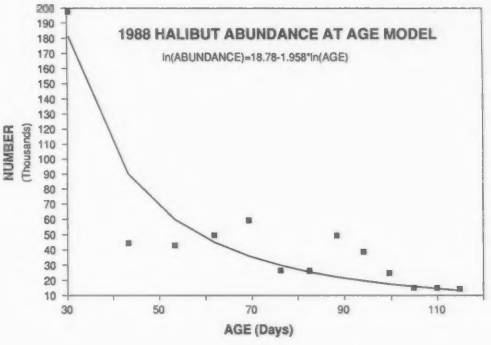


**Figure 9**

Total abundance of juvenile California halibut by age-class summed over both open coast and bay habitats, with the fitted model used to estimate mortality rates.

**Table 3**

Sum of squared deviations (SS) between observed and calculated or transformed abundance-at-age predicted from seven regression models applied to abundance-at-age for juvenile California halibut from 1988.

| Model | Residual SS ($\times 10^9$) |
|---|---|
| 1 Survival rate (SR) increases linearly<br>SR = 0.264 + 0.0072 * age | 6.48 |
| 2 Survival rate increases exponentially<br>SR = 0.174 * exp((0.0070 * age) + 1.0035) | 7.99 |
| 3 Survival rate asymptotic<br>SR = 0.025 * age * exp(−0.897) | 7.49 |
| 4 Daily production<br>ln(daily production) = 17.1 − 1.54 * ln(age) | 12.09 |
| 5 Daily production<br>ln(daily production) = 9.55 − 0.0123 * age | 12.60 |
| 6 Log-transformed abundance on age<br>ln(abundance) = 12.3 − 0.0229 * age | 10.87 |
| 7 Log-transformed abundance on ln(age)<br>ln(abundance) = 18.78 − 1.958 * ln(age) | 4.38 |

Lagoon ($N_{\text{Mission Bay}}$ 42,067, SE 8543; $N_{\text{Agua Hedionda Lagoon}}$ 14,432, SE 3312), but there was a second large peak in Mission Bay for individuals at about 90 days ($N$ 43,697, SE 7850) (Fig. 8).

The class composed of transforming larvae (age 30 days) was the most abundant age class on the open coast in 1988 ($N$ 191,553, SE 17,339) (Fig. 8). Abundance rapidly decreased with age on the open coast, with essentially no halibut 70–180 days of age present on the open coast (Fig. 8). The decline in abundance of halibut on the open coast corresponded to an increase in the bays (Fig. 8).

## Mortality

Total age-specific abundance was determined by combining data from the bay and open coast habitats (Fig. 9). In the survey area, the total loss of juvenile halibut ages 30–115 days was estimated at 183,250 (95% CL of 148,800 and 210,350) (Fig. 9).

Instantaneous mortality rates ($z_{(t)}$) were calculated by age-class using abundance-at-age, with age obtained from the linear regression of ln-transformed abundance on ln(age) (Table 3, Fig. 9), and the duration of each age-class calculated from the age-at-size relationship (Table 4) (Lo 1985). Instantaneous mortality rates ($z_{(t)}$) were highest (0.044) for the youngest juveniles, and decreased with increasing age but became constant ($\bar{x}$ 0.0124, SD 0.001) for juveniles 70 days of age and older (Table 4).

I also calculated habitat-specific instantaneous mortality rates ($z_{(t)}$) for juveniles ≤70 days of age that were taken only on the open coast, and for those 88–115 days of age taken only in the bays (i.e., immigration completed (Table 5).

The apparent mortality in bays was much higher than that predicted from the combined bay and coast data, ranging from 0.043 to 0.037 for the bay model and from 0.011 to 0.014 for the total mortality model (Tables 4, 5). The age-specific mortality of halibut from the bays declined with increasing age, and was not constant as predicted by the total mortality model (Tables 4, 5).

To test for differences between the age-specific instantaneous mortality rates ($z_{(t)}$) of the total population, and of the open coast and bays, I used ANCOVA on the age-specific mortality coefficient, Beta. Beta is related to the instantaneous mortality rate ($z_{(t)}$) by the equation: $z_{(t)}$ = Beta/t (Lo 1985). The Beta coefficients for the total population (1.94, SE 0.22) and the open coast juveniles (ages ≤70 days, Beta 3.58, SE 1.10) were significantly different ($P \leq 0.01$) (Table 6). The difference in the Beta coefficient between juvenile halibut on the open coast and the total halibut abundance-at-age is probably due to movement of halibut from the coast to the bays. Nearly half of the decline in abundance of juveniles along the coast could be caused by their movement into the bays (1.94/3.58 = 0.54). The Beta coefficients for the total population and the bay juveniles (ages 94–115 days) also differed significantly ($P \leq 0.05$), with a Beta of 0.69 (SE 0.77) for the total population, and 2.96 (SE 0.65) for the juveniles from the bays (Table 6). Mortality rates in the bays appear to be underestimated by the abundance-at-age model for the total halibut population.

**Table 4**

Instantaneous mortality rates for the 1988 year-class of juvenile halibut <115 days ($z(t_i)$) by age in days ($t_i$) computed from daily juvenile production estimates ($P_{ti}$) and age ($t_i$) for 1988. Daily production estimates were obtained from log-linear model estimates of abundance-in-age classes adjusted for the number of days juveniles remained in the age-class. Percent of the total population in the bays by age-class is also given.

| Length-class (SL, mm) | Age-class ($t_i$) (days) | Estimated abundance ($n$) | Percent in bays | Estimated daily production | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | $P_{ti}$ | $P_{ti-1} - P_{ti}$ | $t_i - t_{i-1}$ | $t_i = (t_i + t_{i-1})/2$ | $z(t_i)$ |
| ⩽10 | 30.3 | 181385.1 | 3.08 | 18138.5 | | | | |
| 11–15 | 43.3 | 90161.8 | 40.37 | 7706.1 | 10432.4 | 13.0 | 36.8 | 0.044 |
| 16–20 | 53.3 | 60025.3 | 69.92 | 6454.3 | 1251.8 | 10.0 | 48.3 | 0.016 |
| 21–25 | 61.8 | 44927.3 | 86.16 | 5615.9 | 838.4 | 8.5 | 57.5 | 0.015 |
| 26–30 | 69.3 | 35901.3 | 95.24 | 5056.5 | 559.4 | 7.5 | 65.5 | 0.013 |
| 31–35 | 76.2 | 29812.5 | 100.00 | 4586.5 | 469.9 | 6.9 | 72.7 | 0.013 |
| 36–40 | 82.5 | 25518.1 | 95.93 | 4183.3 | 403.2 | 6.3 | 79.3 | 0.013 |
| 41–45 | 88.4 | 22290.1 | 98.13 | 3910.5 | 272.7 | 5.9 | 85.4 | 0.011 |
| 46–50 | 94.1 | 19723.2 | 93.30 | 3586.0 | 324.5 | 5.7 | 91.2 | 0.014 |
| 51–55 | 99.5 | 17681.8 | 95.68 | 3336.2 | 249.8 | 5.4 | 96.8 | 0.012 |
| 56–60 | 104.8 | 15973.4 | 96.17 | 3132.0 | 204.2 | 5.3 | 102.1 | 0.011 |
| 61–65 | 109.9 | 14554.3 | 100.00 | 2910.8 | 221.2 | 5.1 | 107.3 | 0.013 |
| 66–70 | 114.9 | 13340.1 | 100.00 | 2722.4 | 188.4 | 5.0 | 112.4 | 0.012 |

**Table 5**

Habitat-specific instantaneous mortality rates of juvenile halibut <115 days ($z(t_i)$) by age in days ($t_i$) computed from daily juvenile production estimates ($P_{ti}$) and age ($t_i$) for 1988. Halibut 30.3–69.3 days of age were from the open coast habitat, and halibut ⩾88.4 days were from the bays. Daily production estimates were obtained from log-linear model estimates of abundance by habitat adjusted for the number of days juveniles remained in each age-class.

| Habitat | Age-class ($t_i$) (days) | Estimated abundance ($n$) | Estimated daily production | | | | |
|---|---|---|---|---|---|---|---|
| | | | $P_{ti}$ | $P_{ti-1} - P_{ti}$ | $t_i - t_{i-1}$ | $t_i = (t_i + t_{i-1})/2$ | $z(t_i)$ |
| Open coast | 30.3 | 185384.8 | 18538.5 | | | | |
| | 43.3 | 32540.9 | 2781.3 | 15757.2 | 13.0 | 36.8 | 0.065 |
| | 53.3 | 11820.4 | 1271.0 | 1510.3 | 10.0 | 48.3 | 0.054 |
| | 61.8 | 5746.9 | 718.4 | 552.6 | 8.5 | 57.5 | 0.051 |
| | 69.3 | 3288.5 | 463.2 | 255.2 | 7.5 | 65.5 | 0.048 |
| | 76.2 | | | | | | |
| | 82.5 | | | | | | |
| Bays | 88.4 | 45824.8 | 8039.4 | | | | |
| | 94.1 | 33279.7 | 6050.9 | 1988.6 | 5.7 | 91.2 | 0.043 |
| | 99.5 | 25010.6 | 4718.9 | 1331.9 | 5.4 | 96.8 | 0.041 |
| | 104.8 | 19175.6 | 3759.9 | 959.1 | 5.3 | 102.1 | 0.038 |
| | 109.9 | 15035.1 | 3007.0 | 752.9 | 5.1 | 107.3 | 0.039 |
| | 114.9 | 11972.7 | 2443.4 | 563.6 | 5.0 | 112.4 | 0.037 |

Bay abundance-at-age estimate: $\ln(\text{abundance}) = 33.68 - 5.12 * \ln(\text{age})$ (residual SS = $4.567 \times 10^7$).
Open coast abundance-at-age estimate: $\ln(\text{abundance}) = 28.76 - 4.87 * \ln(\text{age})$ (residual SS = $6.219 \times 10^7$).

**Table 6**

Analysis of covariance (ANCOVA) on the age-specific mortality rate Beta by habitat, where Beta is defined by the relationship between the instantaneous mortality rate and age ($z_t$ = Beta/t).

| Covariates | $N$ | Age range (days) | Beta | SE | $F$ | $P$ |
|---|---|---|---|---|---|---|
| Total population | 4 | 43–69 | 1.94 | 0.22 | 19.62 | <0.01 |
| Coast population | 4 | 43–69 | 3.58 | 1.10 | | |
| Total population | 5 | 94–115 | 0.69 | 0.76 | 8.31 | <0.05 |
| Bay population | 5 | 94–115 | 2.96 | 0.65 | | |

### Rate of movements into bays

I estimated the proportion of the population by age-class emigrating each day from the open coast to the bays by calculating the difference between the percentage of juvenile halibut lost daily from the total population and from the open coast using age-specific instantaneous mortality rates (Tables 4, 5) in the following equation:

$$\% \text{ emigrating/day} = ((1 - e^{-z(\text{total population})} - (1 - e^{-z(\text{open coast})})) \times 100.$$

The decline in abundance of juvenile halibut on the open coast between days 30 and 70 was 182,100, and for the total population was 145,500 (Tables 4, 5). During this time, the daily emigration rate increased from 1.99% for juveniles from age 30–43 days, to 3.67% from age 43–53 days, then declined slightly to 3.35% by 70 days.

## Discussion

### Extent of bay utilization

Juvenile halibut appear to be dependent upon bays as nursery areas, since nearly all halibut between 76 and 115 days of age occurred in the bays rather than the open coast (Fig. 8). Transforming larvae and newly-settled juvenile halibut ≤70 days old occurred on the open coast (97% of the transforming larvae were on the open coast), but over 95% of the total population of halibut >70 days were in the bays (Table 4).

An alternative explanation for the decline in abundance of juvenile halibut on the open coast is that they move somewhere other than the bays, or suffer heavy mortality. If halibut moved offshore, one would expect a positive relationship between size of juvenile halibut (31–70 mm SL, or 76–115 days) and bottom depth. This is contrary to the observed size-structured distribution pattern (Fig. 7). The decrease in abundance of juvenile halibut on the open coast may have included higher in situ mortality rates, but the corresponding increase in abundance in the bays suggests that movement from the coast to the bays probably accounts for about half of the coastal decline.

### Advantage of bays as nursery areas

**Growth** The potential advantages of using bays as nursery areas are increased growth and decreased mortality. Increased growth was not observed for juvenile English sole *Parophrys vetulus* in Oregon estuaries: they grow at about the same rate as juveniles on the Oregon coast, but were more variable in size-at-age than those on the coast (Rosenberg 1982). Similarly, growth rates of juvenile California halibut ≤40 mm SL on the coast and in the bays were not significantly different.

California halibut 70–120 mm SL grew faster than all other length-classes with rates approaching 1 mm/day (Fig. 6). These fast and variable growth rates occurred during the period when juvenile halibut occurred only in the bays (>115 days of age). Unfortunately, comparisons could not be made between open coast and bay habitats during this period of fast growth, which coincides approximately with a change in the food habits of halibut >55 mm SL, from a diet composed primarily of small crustaceans (copepods, amphipods, mysids, and cumaceans) to one composed of an increasing proportion of fish by weight (mostly gobies) (Haaker 1975, Allen 1988, Drawbridge 1990). Juvenile halibut feeding on gobies in the laboratory remain partially buried in the substrate, only striking at gobies passing within a distance of three headlengths (Haaker 1975). Gobies are abundant in bays (mean density of *Ilypnus gilberti* in Mission Bay, 8.1/m$^2$), but not in shallow coastal waters <30 m (Brothers 1975, Allen 1985, Plummer et al. 1983). The diet of larger juvenile halibut becomes increasingly piscivorous: juvenile halibut >150 mm SL on the open coast eat primarily northern anchovies by weight (Plummer et al. 1983, Allen 1982).

**Predation risk** Predation risk may be higher for small halibut on the open coast than in the bays. At least six fish species on the open coast are known to eat flatfishes: these include California halibut, thornback ray *Platyrhinoidis triseriata*, fantail sole *Xystreurys liolepis*, bigmouth sole *Hippoglossina stomata*, speckled sanddab *Citharichthys stigmaeus*, and California lizardfish *Synodus lucioceps* (Ford 1965, Allen 1982). Ford (1965) found many small halibut (TL <10 mm) in the stomach contents of thornback rays, with a maximum of 15 newly-settled halibut in the stomach of one ray alone. The combined density of rays *Platyrhinoidis triseriata*, *Urolophus halleri*, and *Gymnura marmorata*) on the shallow open coast (<10 m) is about 100/hectare (Ford 1965). Speckled sanddab is the most abundant flatfish in shallow open coast waters, with a mean density of 950/hectare at Torrey Pines (Ford 1965, Allen 1982, Love et al. 1986, DeMartini and Allen 1984, Kramer 1990). Although the diet of speckled sanddab is composed primarily of mysids, they are probably capable of eating newly-settled halibut, since small unidentified flatfish juveniles have been found in their stomachs (Ford 1965).

In the bays, two potential predators include the round stingray *Urolophus halleri*, and the staghorn sculpin *Leptocottus armatus* (Allen 1985, Tasto 1975, Babel

1967). Both occur along the shallow open coast as well, but are most abundant in bays (Allen 1985). Staghorn sculpin feed primarily on crustaceans (>50% by weight), but small diamond turbot *Hypsopsetta guttulata* have also been found in their stomachs (frequency of occurrence 0.5%) (Tasto 1975). Over 94% of the diet by volume of round stingray is composed of molluscs, polychaetes, and crustaceans, but gobies also have been found in their stomachs (Babel 1967).

Other predators found both in the bays and on the open coast include barred sand bass *Paralabrax nebulifer*, spotted sand bass *P. maculatofasciatus*, and kelp bass *P. clathratus*. Spotted sand bass occur predominantly in bay habitats, barred sand bass occur ubiquitously in the bays and on the open coast, and kelp bass are associated with rock reef and kelp bed habitats on the open coast, but also have been taken as juveniles in bays (Allen 1985, Lane 1975). Kelp bass on the open coast feed mostly on northern anchovies and crabs, and have been found occasionally with flatfishes in their stomachs (Quast 1968). The diet of barred sand bass taken from bottom depths of 8–30 m on the open coast indicates that they forage close to the substrate, feeding on brachyuran crabs, mysids, pelecypods, and epibenthic fishes (mostly *Porichthys notatus*) (Roberts et al. 1984, Feder et al. 1974). Spotted sand bass occur predominantly in bay habitats, feeding on crabs and other crustaceans, and on small kelpfish (Feder et al. 1974, Allen 1985). The juveniles of all three species are found commonly in Mission Bay, and are considered highly probable goby predators (Brothers 1975). The sand basses probably eat juvenile halibut also, as gobies and halibut share the same habitats.

Comparison of predation risk must also include a measure of abundance or biomass of predators by habitat. The estimated density of the potential bay predators (round stingray, *Paralabrax* spp., and staghorn sculpin) based on otter trawl surveys is 61/hectare in Agua Hedionda Lagoon, and only 3/hectare on the open coast (San Diego Gas and Electric 1980). The estimated density of two open-coast predators, the speckled sanddab and the thornback ray, is >1000/hectare (Ford 1965). Based on this scanty information, it appears that predators are more abundant on the open coast than in the bays.

Thus the possible advantages of using bays as nursery areas by juvenile halibut appear to be at least twofold: (1) Decreased risk of predation on newly-settled juveniles, since fewer predators are known to occur there; and (2) increased potential for faster growth of juveniles >55 mm SL because small fishes (gobies) are more abundant in bays than on the open coast (Haaker 1975, Allen 1985).

## Migration to bays

The migration of larvae from spawning areas over the continental shelf to their juvenile nursery areas in embayments is thought to consist of two phases (Boehlert and Mundy 1988): Accumulation of larvae in the nearshore zone (Boehlert and Mundy 1988, Miller et al. 1986), and location and entering of the bays by transforming larvae and juveniles (Boehlert and Mundy 1988). The nearshore accumulation of larvae prior to movement to the bays is probably facilitated by the timing of spawning, the short duration of pelagic stages, and the vertical distributions of the postflexion and transforming larval stages. California halibut spawn throughout the year, with peak spawning during the winter and spring (Lavenberg et al. 1986, Walker et al. 1987). The spawning peak coincides with the period of minimum offshore transport of surface water in the Southern California Bight (Parrish et al. 1981, Jackson 1986). Offshore transport increases in late spring and summer due to increasing upwelling activity (Parrish et al. 1981, Jackson 1986). The seasonal shift in upwelling activity has been correlated with a seasonal cross-shelf shift in the zooplankton assemblage off San Onofre: from February to early April the community was shifted onshore, and from mid-April to July the shift was offshore, corresponding to the period of increased upwelling (Barnett and Jahn 1987).

The size distribution of California halibut larvae taken in plankton tows indicates that they move inshore as they approach metamorphosis. Preflexion and flexion larvae (~2–6 mm SL) occur in midwater >2 km offshore, whereas transforming larvae occur at night in the neuston within 1 km of shore (Moser and Watson 1990). My collections indicated that transforming larvae occur on the bottom during the day; thus transforming larvae appear to undergo a daily vertical migration, occurring at the surface at night and at the bottom during the day. Larvae of other *Paralichthys* species, yellowtail flounder *Limanda ferruginea*, stone flounder *Kareius bicoloratus*, and the larval stages of several crustacean taxa have similar diurnal activity patterns (Weinstein et al 1980, Tsuruta 1978, Shanks 1988, Penn 1975, Smith et al. 1978).

Postflexion and transforming halibut larvae may be transported shoreward by internal waves at night when they are in the neuston, with very little movement during the day while they are on the bottom, resulting in accumulation of larvae nearshore (Moser and Watson 1990). Surface slicks associated with internal waves may transport neustonic larval fishes and crustaceans onshore (Shanks 1988, Kingsford and Choat 1986). Recovery of drift bottles released <20 miles offshore in the Southern California Bight region is greatest

between March and October, also suggesting increased onshore transport of surface water (Schwartzlose 1963).

Once nearshore, transforming larvae or settled juveniles may search for bays by using longshore transport (Boehlert and Mundy 1988). Net longshore transport of shallow shelf waters in the Southern California Bight is to the south (Winant and Bratkovich 1981). Longshore current speed measured in shallow water (15 m) averages less than 5 cm/second; at this speed, after 12 hours longshore movement could be as great as 2 km (Winant and Bratovich 1981).

My data on the abundance of transforming larvae and newly-settled juveniles provide an estimate of the time required for halibut to locate and enter the bays from the open coast. The time required can be considered to be equivalent to the difference in the age of peak abundance between the coast and the bays. Halibut reached peak abundance in the bays at an age of about 70 days in 1988, whereas they were most abundant at age 30 days (transformation) on the open coast (Fig. 8). Thus the time required to locate and enter the bays was about 40 days in 1988 (70–30 = 40 days) (Fig. 8). Over a 40-day period, halibut potentially could be transported about 80 km alongshore (40 days × (2 km at 12 hours in the neuston)), which is greater than the total distance between the northern sampling block at San Onofre and Mission Bay (64 km) (Fig. 1). I measured the maximum distance between adjacent bays in southern California at less than 60 km, thus larvae using this transport mechanism would probably encounter a bay within 30 days of reaching the shallow-water coastal environment.

The potential cues used to find the entrances to bays include temperature, currents, odor, turbidity, and bottom substrate (Boehlert and Mundy 1988). A probable cue in southern California is temperature: during spring and summer, when larvae and juveniles are moving into the bays, the temperature is as much as 5°C warmer in the bays than on the open coast (Kramer 1990).

Once a bay entrance is located, the mechanism used to migrate into the bay probably is tidal transport, using incoming tidal currents to aid movement into the bay, and remaining at the bottom to avoid transport out of the bay (Weinstein et al. 1980, Boehlert and Mundy 1988, Fujii et. al. 1989, Tsuruta 1978, Weihs 1978, Runsdorp et al. 1985). To use tidal stream transport to move into bays, individuals must be able to orient to currents, control vertical movements, and remain on the bottom during unfavorable currents. These abilities probably develop by the time larvae reach transformation (Boehlert and Mundy 1988, Weinstein et al. 1980). Only a few tidal cycles may be required for halibut to move from the entrance into the bay. Larval flounder (*Paralichthys* sp.) on the North Carolina coast use tides to augment movement into marshes, migrating to the surface during night flood tides and remaining on the bottom during ebb tides and during the day (Weinstein et al. 1980).

In conclusion, California halibut settle either in bays or on the open coast, but ultimately nearly all halibut settling on the coast enter and use the bays as nursery areas during their first year of life. The advantages of bays as nursery areas may be a decrease in risk of mortality of newly-settled halibut, and an increase in growth of larger juveniles that feed upon the abundant small fishes in the bays.

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**Abstract.**—The larvae and juveniles of two platytroctid species, *Holtbyrnia latifrons* and *Sagamichthys abei*, from the northeastern Pacific are described. Young individuals were collected at a broad range of mesopelagic depths, indicating that they occupy similar depths as adults. The relatively large larvae (~15 mm) have well-developed teeth and fins while carrying the yolksac. Presence of <20 mm sizes from most months of the year may indicate year-round spawning.

# Description of Young of the Mesopelagic Platytroctids *Holtbyrnia latifrons* and *Sagamichthys abei* (Pisces, Alepocephaloidea) from the Northeastern Pacific Ocean

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The only published description of larval platytroctids is that of Beebe (1933). However, Parr (1960) in his review of the family (then known as Searsidae) believed larval platytroctids of 11–17 mm could not be identified even to genus, and showed that Beebe's detailed description of the larvae identified as *Bathytroctes rostratus* was based on several species. In a recent revision of the family, Matsui and Rosenblatt (1987) recognized five species off California. None are congeners. The earliest larvae of the two commonest species, *Holtbyrnia latifrons** and *Sagamichthys abei*, are identifiable by their photophores. This report describes the young of *H. latifrons* and *S. abei* and presents catch data from the Scripps Institution of Oceanography (SIO) Fish Collection and depth of capture data from a series of opening-closing net tows.

## Material and methods

Material used in this study is from the SIO Fish Collection and from samples collected on seven cruises sponsored by the Marine Life Research Group (MLRG) of SIO. Most SIO Fish Collection samples and some from the MLRG cruises were captured in 3-m Isaacs-Kidd midwater trawls (IKMT). Other MLRG collections were made with 2-m Stramin nets and 1-m plankton nets. The 1-m nets were attached to modified Leavitt devices (Leavitt 1938) that allowed the nets to be opened and closed by messengers to sample discrete depth intervals. Their sampling depths were either recorded by TSK depth-distance recorders on the nets and activated when the nets were sampling, or estimated from records taken on a Benthos time-depth recorder attached to the bottom net in the cast. Eight depth intervals from surface to nearbottom were sampled at stations 850–1350 m deep, and 12 depth intervals at stations of 1370 m to ~1800 m. Two samples in the Fish Collection were taken in opening-closing Bongo nets (McGowan and Brown 1966).

A total of 167 (young and adult) *H. latifrons* and 220 *S. abei* were examined in the study. The description of *H. latifrons* is based on measurements and counts of 157 individuals (1 larva, 12 transitional specimens, and 144 juveniles). For *S. abei*, 1 larva, 4 transitional specimens, and 37 juveniles were measured and counted. Samples of *H. latifrons* were gener-

* *Holtbyrnia latifrons* may be a junior synonym of *H. baucoti* Mayer and Nalbant 1972. However *H. baucoti* was inadequately described, and I have failed to gain additional information on the holotype.

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ally collected near the coast at 22–38°N, off the west coast of California and Baja California (but mainly 28–33°N). Samples of *S. abei* were also collected near the coast at 28–38°N, with one individual from 4°N, 142°W.

Most specimens were initially preserved in formaldehyde and later transferred to 70% isopropanol. Length measurements of small specimens were taken with an ocular micrometer of a dissecting microscope and by dividers for larger measurements. All *S. abei* and *H. latifrons* examined had a flexed notochord. Since the notochord extended more than 1 mm beyond the hypurals in the earlier stages, the standard length (SL) measurements of the larvae were taken from the snout to posterior tip of notochord, or to the most posterior extension of the hypurals, whichever was greater.

Head length (HL) measurements were taken from the tip of the snout to the posterior margin of opercle. In individuals with torn or curled gill covers, the anterior base of pectoral fin was substituted as the posterior reference point for HL.

Photophore nomenclature follows Parr (1960) as modified in Matsui and Rosenblatt (1971).

## Key to young platytroctids off California

**1a** Photophores (or melanophores in the shape of photophores) in gular region ($GO_2$; Figs. 1, 2) from yolksac through later juvenile stages ..... 2

**1b** Neither photophores nor patch of melanophores in gular region ..... 3

**2a** Photophores and silvery reflector present on anterior dorsal margin of eye (OO) and on subopercle (SBO) from yolksac stage; intraventral photophore (IVO) present from yolksac stage; opercular opening extending dorsally to about mideye; body coloration generally whitish blue ..... ***Sagamichthys abei***

**2b** OO and SBO photophores absent; IVO appearing near end of yolksac stage; opercular opening extending dorsally to top of eye; epidermal layer lightly pigmented from yolksac stage, becoming dark-brown in juvenile ..... ***Holtbynia latifrons***

**3a** Broad edentulous space between innermost tooth of each premaxilla; small photophore between bases of pelvic fins (IVO) present after yolk is resorbed; gill opening extending dorsally to a level with top of eye ..... ***Maulisia argipalla***

**3b** Only narrow edentulous space between innermost tooth of each premaxilla; photophores absent; gill opening on a level with mideye ..... 4

**4a** Nasal sac nearly bordering maxilla; premaxilla not meeting medially with part extending laterally ..... ***Pellisolus eubranchus***

**4b** Nasal sac midlength of snout; premaxilla meeting medially, with none along lateral margin of mouth ..... ***Mirorictus taningi***

## Description

### *Holtbyrnia latifrons* (Fig. 1)

**Pigmentation** The least developed individual examined has pigmented eyes, pigmentation on the shoulder organ and at the site of the posterior gular organ ($GO_2$); the posterior margin of opercle and the dorsal portion of yolksac are lightly pigmented (Fig. 1A). This is the only specimen examined that is considered a larva; the remaining yolksac stages are already beginning to form the juvenile pigment pattern, and are termed transitional individuals. The most prominent pigmentation in these is the black tissue lining the digestive tract from the mouth and branchial chamber to the anus. Melanophores are concentrated at the dorsal and ventral margins, and on the fins and fin bases. Pigmentation increases with size, and in late juveniles the entire body as well as the head (except for the translucent top of skull) is nearly black in color.

**Morphometrics** The larva (Fig. 1A) has a small head and mouth and an oblong eye that is nearly twice as long horizontally as vertically. The transitional specimen (Fig. 1B) is much more adult-like with the head and eyes nearly doubling in size, and the eyes almost round.

Much of the growth in transition stages is in the head region, and although the body length of 12–17 mm

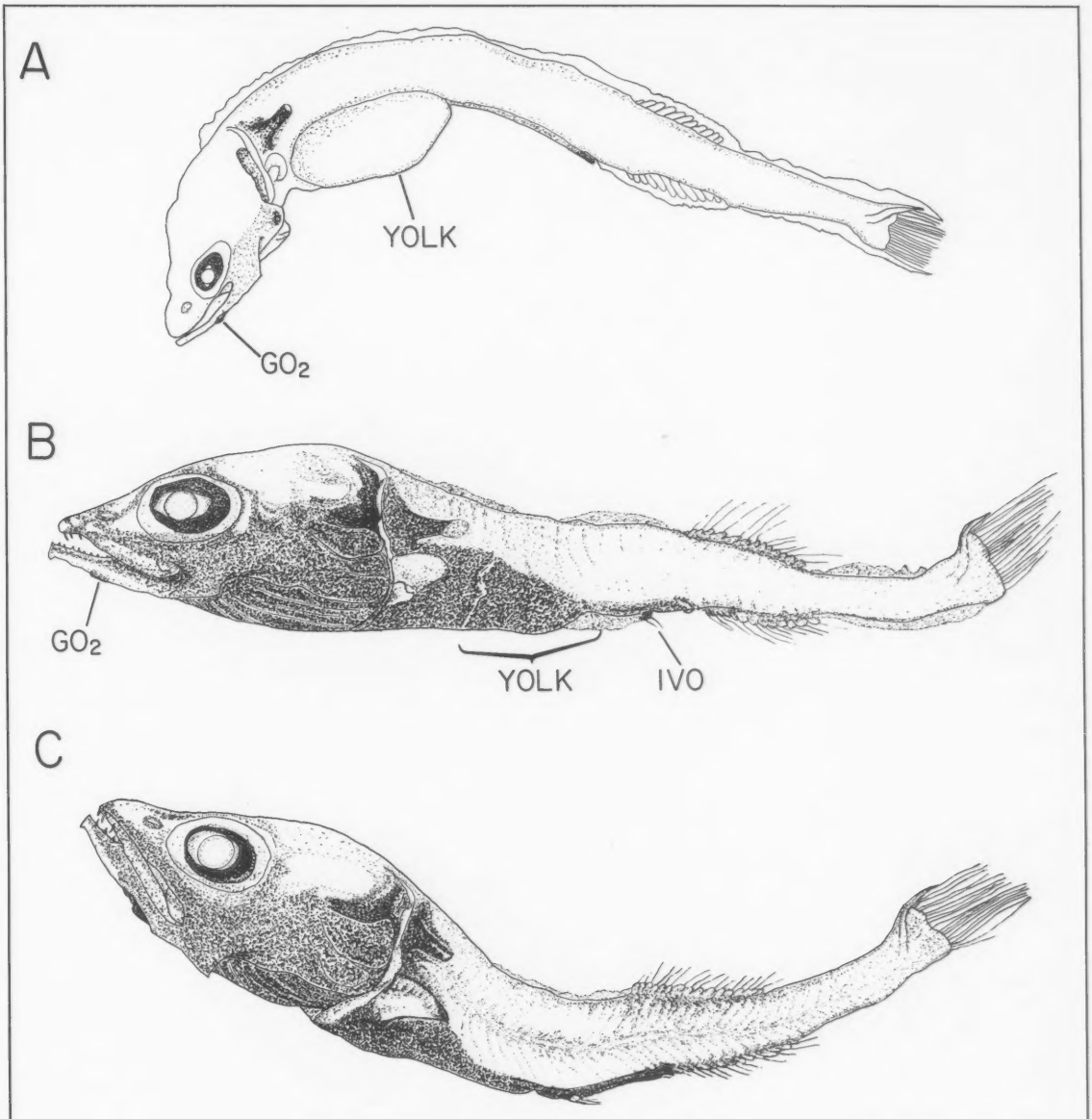


**Figure 1**

Camera lucida drawings of the young of *Holtbyrnia latifrons*: (A) M1-2-1, 15-mm larva; (B) SIO 65-439, 14-mm transitional specimen; (C) 65-443, 14-mm juvenile. $GO_2$ = posterior gular organ; IVO = intraventral organ.

juveniles is shorter than that of the larva, their head length is two times greater (Table 1). Head length increased from 15% of SL in the larva to the adult proportion of 30% of SL at the end of the transitional period. Head length of juveniles is proportionately larger than that of adults even from the earliest stages, measuring 29–37% of SL in the 12–18 mm SL range, with maximum of >40% SL at 36–45 mm SL (Table 2). Head depth increased from 9% SL in the larva, to 10–17% SL in transitional specimens, to 16–23% SL in juveniles as large as 50 mm.

**Table 1**

Measurements (in mm) and counts of *Holtbyrnia latifrons*. SL = standard length, HL = head length, Hd = head depth at angular, asterisks = SIO.

| | Sample no. | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M1-2-1 | M11-1-3 | M2-A7 | M10-1R-2 | M13st1 | *67-62 | *63-447 | *65-439 | *63-447 | *66-398 | *65-443 | M7st3 | *67-101 |
| **Lengths** | | | | | | | | | | | | | |
| SL | 15 | 15 | 15 | 14 | 14 | 13 | 14 | 14 | 14 | 14 | 14 | 16 | 16 |
| HL | 2.3 | 3.8 | 3.3 | 2.4 | 2.3 | 3.0 | 4.2 | 4.8 | 3.8 | 4.3 | 4.5 | 5.1 | 6.0 |
| SL minus HL | 13 | 11 | 12 | 12 | 12 | 10 | 10 | 8.9 | 11 | 9.3 | 9.2 | 10 | 9.7 |
| Hd | 1.4 | 1.4 | 1.7 | 1.4 | 1.2 | 1.4 | 2.0 | 2.3 | 1.8 | 2.2 | 2.4 | 2.7 | 2.9 |
| Yolksac | 3.7 | 3.6 | 3.3 | 3.2 | 3.0 | 3.0 | 2.6 | 2.5 | 2.3 | 0 | 0 | 0 | 0 |
| Eye (long.) | 0.72 | 0.92 | 0.91 | 1.1 | 0.76 | 1.0 | 1.3 | 1.6 | 1.3 | 1.5 | 1.4 | 1.6 | 2.0 |
| Eye (vert.) | 0.48 | 0.60 | 0.58 | 1.0 | 0.44 | 0.52 | 0.83 | 0.83 | 0.52 | 0.83 | 0.92 | 0.75 | 1.2 |
| Maxilla | 1.1 | 1.4 | 1.2 | 1.2 | 1.0 | 1.3 | 1.5 | 2.1 | 1.7 | 1.7 | 2.1 | 2.1 | 2.5 |
| **Counts** | | | | | | | | | | | | | |
| Dorsal rays | 0 | 11 | 15 | 14 | 14 | 12 | 16 | 13 | 16 | 15 | 16 | 18 | 19 |
| Anal rays | 0 | 10 | 13 | 10 | — | 13 | 13 | 13 | 14 | 15 | 14 | 16 | 12 |
| Pectoral rays | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0+2 | 0 | — | 4+? | 4+? | 4+? |
| Branchiostegals | 2 | 4 | 5 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 |
| Gill rakers | 0 | 0 | 0+2 | 0 | 0 | 0+3 | 1+10 | 1+11 | 0+8 | 2+12 | 2+12 | 2+13 | 3+13 |
| Pseudobranchiae | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| Dentition | | | | | | | | | | | | | |
| Vomerine | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 2 | 1 | 2 | 2 | 2 |
| Palatine | 0 | 0 | 0 | 0 | 0 | 0 | 1+1 | 1+1 | 1+1 | 1+1 | 1+2 | 1+1 | 1+1 |
| Basihyal | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| Dentary | 0 | 0 | 3+3 | 0 | 1+1 | 0 | 7+9 | 12+12 | 7+7 | 10+10 | 10+12 | 13+17 | 10+12 |
| Mid-dentary | 0 | 0 | 0 | 0 | 0 | 0 | 1+1 | 0 | 0 | 1+1 | 0+1 | 2+0 | 2+1 |
| Maxillary | 0 | 0 | 0 | 0 | 0 | 0 | 2+1 | 1+1 | 0 | 0 | 0 | 2+1 | 3+3 |
| Premaxillary | 0 | 0 | 0 | 0 | 0 | 1+1 | 2+2 | 3+4 | 4+3 | 3+5 | 4+5 | 5+5 | 4+3 |

**Table 2**

Summmarized counts and morphometrics (% SL) of *Holtbyrnia latifrons*. SL = standard length, HL = head length, Hd = head depth at angular.

| | | | Dentition | | | | | | | | % SL | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SL (mm) | Gill rakers | Pseudo-branchiae | Vomer-ine | Pala-tine | Pre-maxillary | Max-illary | Dentary | Mid-dentary | Basi-hyal | Basi-branchial | HL | Hd | Eye | Max-illary |
| Yolksac | 0–1+0–11 | 2 | 0–2 | 0–1 | 0–4 | 0–2 | 0–12 | 0–1 | 0–1 | 0 | 15–35 | 8–17 | 5–11 | 7–15 |
| 12–15 | 1–3+11–14 | 2 | 1–2 | 1 | 4–5 | 0–5 | 7–12 | 0–2 | 0–1 | 0 | 29–33 | 15–19 | 9–12 | 12–15 |
| 16–20 | 2–5+13–15 | 2–4 | 2–3 | 1–2 | 4–6 | 2–8 | 10–24 | 0–6 | 0–4 | 0 | 29–42 | 14–19 | 7–13 | 11–16 |
| 21–25 | 2–5+13–17 | 2–4 | 2–5 | 1–2 | 4–8 | 5–16 | 15–27 | 0–2 | 0–4 | 0 | 33–39 | 16–20 | 10–12 | 14–17 |
| 26–30 | 5–7+16–19 | 4–5 | 1–2 | 1–2 | 4–9 | 5–19 | 16–30 | 0–5 | 0–3 | 0 | 35–45 | 17–23 | 11–13 | 14–20 |
| 31–35 | 6–7+16–17 | 5 | 2–4 | 1–2 | 7–10 | 5–23 | 15–26 | 0–5 | 0–2 | 0 | 36–39 | 16–19 | 11–12 | 17–20 |
| 36–40 | 6–8+18–19 | 6 | 1–2 | 1–4 | 6–9 | 11–33 | 19–23 | 4–5 | 0–2 | 0–1 | 38–42 | 19–20 | 10–12 | 18–21 |
| 41–45 | 7–9+18–21 | 5–6 | 2–3 | 1–4 | 7–11 | 11–33 | 20–27 | 3–6 | 0–1 | 0–5 | 38–42 | 19–22 | 10–13 | 17–20 |
| 46–50 | 7–8+18–19 | 8 | 2–3 | 1–4 | 10–12 | 15–32 | 33–40 | 2–4 | 0–1 | 0–4 | 36–42 | 19–21 | 10–11 | 18–21 |
| 51–55 | 7+19 | 7 | 2–3 | 2 | 9 | 27–29 | 30–34 | 1–4 | 0–1 | 0–5 | 37 | 20 | 11 | 21 |

Eye length increased from about 5% SL in the larva to as much as 11% SL in some of the transitional specimens and to 11–13% SL in 20–45 mm juveniles. Maxilla length increased from 7% of SL in the larva, to 9–15% SL during transition, to 17–21% SL in 30–50 mm juveniles.

**Fins** All specimens had the notochord flexed with 19 principal caudal rays present. In larvae, narrow finfolds extend anteriorly along the dorsal (to head) and ventral (to anus) body margins. Only the basal parts of the dorsal and anal rays are discernible on the larva (Fig. 1A), but there are 10–13 anal and 11–16 dorsal rays in

the transitional specimens (Table 1). Two pelvic rays are discernible in the most advanced transitional specimen (SIO65-439). Adult counts of dorsal (17–20), anal (14–16), and pelvic (9) fin rays are usually present in 30-mm juveniles. Pectoral fin rays form last, with the first rays appearing at approximately 23 mm SL and adult counts (16–20) by 45 mm SL.

**Branchial region** Branchiostegal rays appear early and only the larval specimen and the least developed transitional specimen had fewer than the adult count of 8.

Gill rakers are absent in the larva, but as many as 12 are on one side of the 1st gill arch in the transitional specimen. Nearly all of these gill rakers are on the lower arch. Only one transitional specimen (SIO65-439) had gill rakers on the 1st epibranchial. The lowest count for juveniles was 1 on the epibranchial and 12 total on the 1st arch, and ranged from 1 to 5 on the upper arch and 12 to 19 total in juveniles <20 mm SL. The smallest individual with the adult gill raker count of 25 was 27 mm SL and all individuals 42 mm and larger had counts in the adult range of 25–30.

Medial gill rakers of the 3d and 4th arches are in an uninterrupted row in juveniles as small as 19 mm, but no medial gill rakers form on the 1st and 2d arches until after 20 mm. By 45 mm SL, there are about 6 medial rakers on the epibranchial and on the ceratobranchial of the 2d arch, and 5 on these elements of the 1st arch.

There are 2 pseudobranchiae in the larva and transitional specimens. The smallest individual with a 3d pseudobranchium measured 17 mm and the smallest with a 4th was 20 mm. No specimen <50 mm SL had attained the highest adult count of 8. Counts varied as much as 4 between individuals of similar lengths.

**Dentition** In the study material, only the larva is toothless. Teeth on dentary, premaxilla, maxilla, vomer, palatines, basihyal, and on the lateral face of the dentary (mid-dentary teeth) appear during transition. Teeth are easily dislodged, contributing substantially to individual variation in counts. The most advanced transitional specimen (SIO65-439; Table 1) had a single medial tooth on the basihyal, a tooth on each palatine, and a total of 7 premaxillary, 2 maxillary, 24 dentary, and 2 vomerine teeth. Only one transitional specimen had mid-dentary teeth. There are fewer maxillary than dentary teeth in the early stages, but this gradually changes and the numbers are about even in individuals 25 mm and larger (Table 2). Highest count of premaxillary teeth among transitional individuals was 4 on a side. The numbers increased to 4–6 in 13–20 mm juveniles, with counts as high as 10 at 50 mm SL. The inner pair of premaxillary teeth point horizontally beginning from about 25 mm SL. Frequently, a second smaller tooth forms adjacent to the 1st.

Mid-dentary teeth are probably more susceptible to damage than other dentition and most individuals smaller than 30 mm were without them, although counts of 4 on one side occurred as early as 17 mm. Individuals 30–50 mm long usually had 4–5 mid-dentary teeth. In the youngest stages, a single tooth was usually present on each palatine. The number variably increased to as many as 4 in individuals over 30 mm. Most prejuveniles and early juveniles had a medial tooth on the basihyal, with occasional individuals with 2–4 in a medial row. Basibranchial and mesopterygoid teeth appeared after 40 mm, and ectopterygoid teeth were only found in the adults.

**Photophores** Photophores of young platytroctids are oriented horizontally (Matsui and Rosenblatt 1971). The posterior gular organ ($GO_2$; Fig. 1) is the only photophore present during most of the yolksac stage. It is an opaque spot outlined by dark pigment in the larva, and forms at the posterior, narrow end of a black, conically-shaped pouch. Near the end of the yolksac stage, the intraventral organ (IVO) develops inside a silver-lined, anteriorly facing pouch. The photophore at the subopercle (SBO) appears later in juveniles. However, it is considered rudimentary as it is surrounded by opaque tissue and is without an anterior opening. These photophores are covered over and lost in larger individuals.

Additional photophores begin appearing in some juveniles of 26 mm but are uncommon until after 28 mm. Unlike earlier photophores, they face ventrally and persist in adults. Earliest to appear are (1) a transversely barred thoracic organ (THO) located on the ventral body margin midway between the pectoral and pelvic fins, (2) two elliptical supraventral organs (SVO) located anterolateral to the bases of the ventral fins, and (3) two elliptical supraanal organs (SAO), lateral to the anal opening. Other adult photophores appear soon after and include a transversely barred midventral organ (MVO) located anteroventral to the SVO, the elliptical branchiostegal organs (BRO), the infracaudal organ (ICO) located on the ventral margin of the caudal peduncle, the pectoral organ (PO) located on the ventralmost ray of pectoral fins, and a longitudinally barred jugular organ (JO) located between the bases of the pectoral fins. All adult photophores are usually present by 50 mm.

### *Sagamichthys abei* (Fig. 2)

**Pigmentation** The single larval specimen is nearly unpigmented. Most heavily pigmented areas are the eye, shoulder organ, subopercular photophore (SBO),

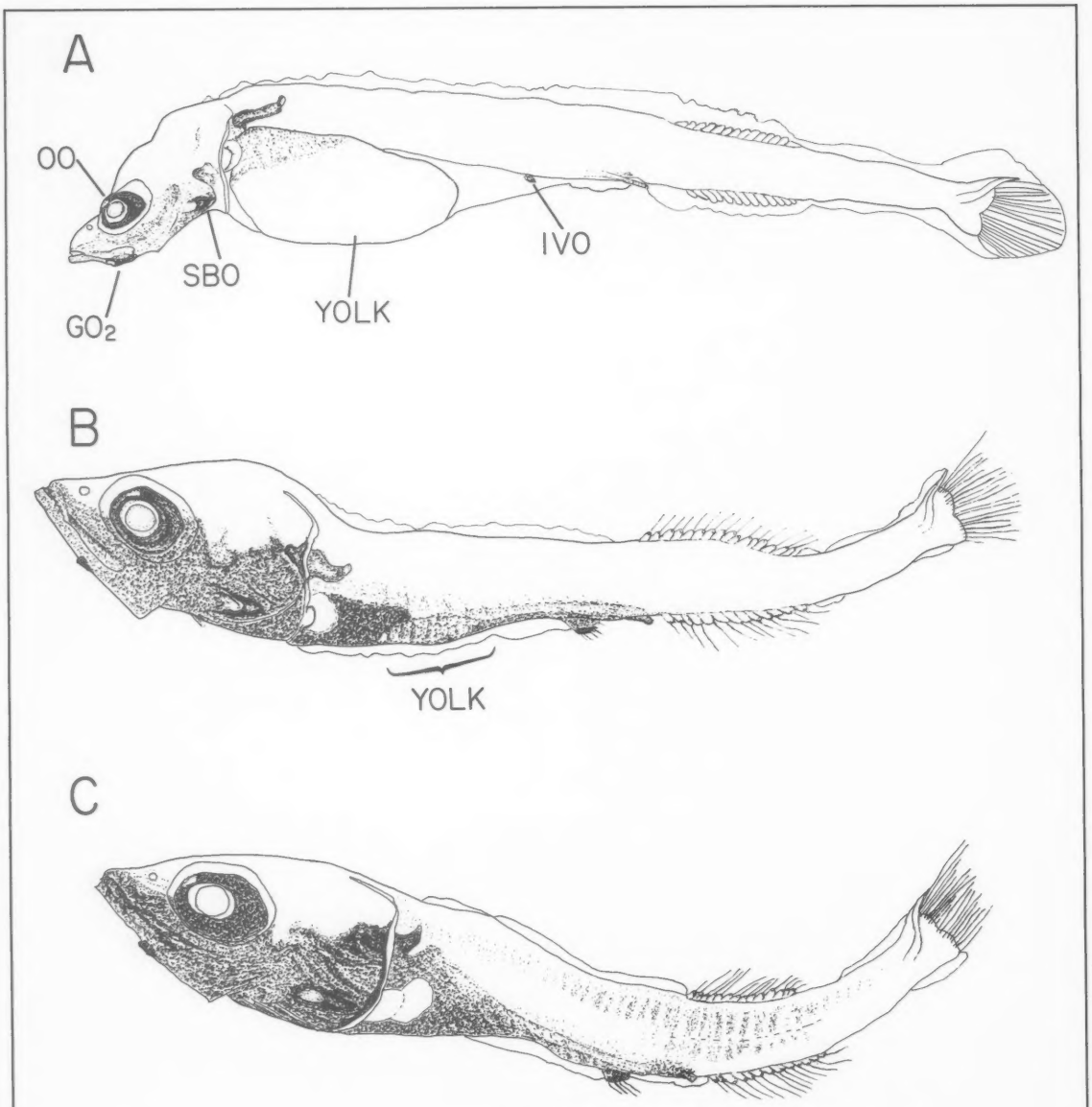


**Figure 2**

Camera lucida drawings of the young of *Sagamichthys abei*: (A) M13-1A, 16-mm larva; (B) SIO66-390, 14-mm transitional specimen; (C) M7 Sta 3, 16-mm juvenile. OO = orbital organ; $GO_2$ = posterior gular organ; SBO = subopercular organ; IVO = intraventral organ.

and posterior gular photophore ($GO_2$), with light pigmentation in the mouth, gill chamber, and on the dorsal region of the yolksac.

In the transitional specimen, the mouth, stomach cavity, and intestine are lined with black tissue. These blackened areas show through the translucent musculature, darkening the ventral half of the head and body anterior to the vent. Muscles between the anal and dorsal fins take on a bluish-black tinge, which spreads anteriorly and posteriorly from that area in larger individuals, with the area around the caudal peduncle darkening last. Among the more advanced transitional

**Table 3**

Measurements (in mm) and counts of *Sagamichthys abei*. SL = standard length, HL = head length, Hd = head depth at angular; asterisks = SIO.

| | Sample no. | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M13st1A | M4-st1 | *66-390 | *66-390 | *66-422 | *63-165 | M7-st3 | *66-371 | *70-8 | *65-439 | *57-41 | *75-472 | *54-122 |
| **Lengths** | | | | | | | | | | | | | |
| SL | 16 | 16 | 14 | 14 | 14 | 13 | 16 | 16 | 16 | 17 | 17 | 18 | 20 |
| HL | 2.8 | 4.2 | 4.5 | 4.7 | 4.5 | 3.7 | 5.3 | 5.1 | 5.0 | 5.9 | 5.5 | 5.8 | 7.2 |
| SL minus HL | 13 | 12 | 9.5 | 9.3 | 9.5 | 9.3 | 11 | 11 | 11 | 11 | 12 | 12 | 13 |
| Hd | 1.5 | 2.0 | 2.3 | 2.3 | 2.1 | 2.1 | 2.7 | 2.3 | 2.6 | 2.4 | 2.4 | 2.3 | 3.2 |
| Yolksac | 4.0 | 4.2 | 2.5 | 2.5 | 3.2 | 2.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Eye (long.) | 0.92 | 1.1 | 1.1 | 0.92 | 1.0 | 0.76 | 1.7 | 1.8 | 1.3 | 1.7 | 1.3 | 1.6 | 2.2 |
| Eye (vert.) | 0.54 | 0.58 | 0.64 | — | 0.72 | 0.60 | 1.2 | 0.83 | 0.80 | 1.2 | 1.2 | 1.2 | 1.6 |
| Maxilla | 1.1 | 1.5 | 1.8 | — | 1.7 | 0.92 | — | 2.2 | 2.1 | 2.4 | 2.4 | 2.3 | 3.0 |
| **Counts** | | | | | | | | | | | | | |
| Dorsal rays | 0 | 16 | 16 | 14 | 13 | 13 | 14 | 16 | 14 | 16 | 15 | 16 | 15 |
| Anal rays | 0 | 14 | 13 | 14 | 13 | 12 | 14 | 15 | 13 | 15 | 14 | 14 | 14 |
| Pectoral rays | 0 | 0 | 3 | 0 | 3 | 0 | 5 | — | 5 | 7 | 4 | 7 | 5 |
| Branchiostegals | 0 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 |
| Gill rakers | 0 | 0+9 | 0+10 | 0+11 | 0+8 | 0+7 | 1+12 | 1+11 | 3+13 | 2+11 | 2+10 | 3+12 | 3+13 |
| Pseudobranchiae | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 |
| Dentition | | | | | | | | | | | | | |
| Vomerine | 0 | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 |
| Palatine | 0 | 1+0 | 0 | 1+1 | 1+0 | 1+1 | 1+1 | 1+1 | 0 | 1+1 | 1+1 | 1+1 | 1+0 |
| Basihyal | 0 | 1 | 3 | 3 | 1 | 1 | 4 | 1 | 4 | 7 | 4 | 6 | 5 |
| Basibranchial | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 4 | |
| Dentary | 0 | 3+? | 3+5 | 7+? | 8+? | 5+5 | ?+14 | 10+8 | 15+11 | 17+? | 14+15 | 17+? | 12+? |
| Mid-dentary | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3+2 | 4+? | 2+3 | 2+? | ?+3 |
| Maxillary | 0 | 0 | 0 | 0 | 0 | 0 | 4+6 | — | 9+6 | 10+? | 9+? | 11+14 | 12+? |
| Premaxillary | 0 | 2+? | 3+3 | — | 1+1 | 2+? | 6+5 | 7+7 | 5+5 | ?+5 | 5+5 | 6+8 | 8+? |

specimens, sparse epidermal pigment is found around the lower jaw, with a broken line at the midline between the anal and dorsal fins. This pigmentation spreads and intensifies in the juveniles, resulting in the blue-gray to black coloration.

**Morphometrics** A large yolk mass extends from the cleithrum to about halfway to the anus in the single larval specimen, which has a small head (headlength = 17% of SL) and mouth and undeveloped fins. Head length in transitional specimens nearly doubles to 26–33% of SL. Maxillary length increased from 7% SL to 9–13% SL during transition. Body length shortened or remained about the same (Table 3), as body length behind the head shortened. Head length and depth in transitional specimens are similar proportionately to adults, but the mouth is smaller than in adults and extends only to mideye, instead of behind the eye. Maxillary length is 9–13% SL during transition and 14–16% SL in adults. Eye length in the larva is proportionately similar to eye diameter in adults; however, eye depth is only half of the length in the former.

Head, mouth, and eye are proportionately largest in the 20–60mm juveniles. Head length was mainly 35–38% of SL at this range (Table 4) but <30% of SL in individuals larger than 150mm SL.

**Fins** All specimens have a flexed notochord and 19 principal caudal rays. Dorsal and anal fin rays are absent in the larval specimen, but pterygiophores of 11 anal and 13 dorsal rays are present. Counts of 13–16 dorsal, and 12–15 anal rays of the transitional specimens (Table 3) were nearly in the adult range of 16–18 dorsal and 14–16 anal finrays. Most juveniles over 20mm SL had the adult counts. Pectoral fin rays are absent in specimens <18mm. There were 0–7 pelvic rays at that length. Adult counts on all fins are found in juveniles >30mm SL. There are 9–10 (usually 9) pelvic and 14–18 pectoral fin rays in the adult.

**Branchial region** Branchiostegal rays and gill rakers are absent in the larval specimen. Except for one individual with 7 rays, transitional specimens have the adult count of 8 branchiostegal rays. There are 8–11

**Table 4**

Summarized counts and morphometrics (% SL) of *Sagamichthys abei*. SL = standard length, HL = head length, Hd = head depth at angular.

| | | | Dentition | | | | | | | | % SL | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SL (mm) | Gill rakers | Pseudo-branchiae | Vomer-ine | Pala-tine | Pre-maxillary | Max-illary | Dentary | Mid-dentary | Basi-hyal | Basi-branchial | HL | Hd | Eye | Max-illary |
| Yolksac | 0+0–11 | 2 | 0–2 | 0–1 | 0–3 | 0 | 3–8 | 0 | 0–3 | 0 | 18–33 | 9.3–16 | 6–8 | 7–13 |
| 16 | 1–3+11–13 | 2–3 | 2 | 1 | 5–7 | 6–9 | 10–15 | 0–3 | 0–4 | 0 | 31–33 | 14–16 | 8–15 | 13–14 |
| 17–20 | 2–4+11–13 | 2–3 | 2 | 1 | 5–9 | 7–14 | 12–18 | 1–4 | 4–8 | 0–8 | 32–43 | 14–21 | 8–11 | 13–18 |
| 21–25 | 3–5+13–15 | 3 | 2 | 1–3 | 8–9 | 7–19 | 12–25 | 1–3 | 4–8 | 2–9 | 34–35 | 15–18 | 9–10 | 14–16 |
| 26–30 | 4+15 | 4 | 3 | 2 | 13 | 19 | 17 | 5 | 9 | 10 | 35 | 16 | 10 | 16 |
| 31–35 | 4–5+15–16 | 4 | 2 | 2–5 | 9–11 | 17–26 | 15–19 | 3–5 | 6–12 | 6–9 | 34–36 | 16–22 | 8–10 | 14–15 |
| 36–40 | 6+16 | 4–5 | 2–5 | 2–3 | 10–14 | 25–28 | 16–22 | 6–9 | 5–9 | 4–6 | 30–39 | 17–20 | 9–11 | 16–18 |
| 41–45 | 6–7+17–18 | 5 | 2 | 2 | 11–12 | 28–29 | 28 | 6 | 3–7 | 6 | 32–36 | 8–16 | 7–9 | 15–19 |
| 46–50 | 6–7+15–16 | 6 | 2 | 2 | 11–12 | 34–35 | 22 | 6–7 | 5 | 6 | 34–38 | 18–20 | 9–10 | 17–20 |
| 51–55 | 7+19 | 7 | 2 | 2 | 17 | 41 | 26 | 10 | 7 | 14 | 41 | 22 | 9 | 20 |
| 56–60 | 7+16 | 6–7 | 2 | 2 | 13 | 37 | 23 | 9 | 2 | 9 | 35 | 20 | 8 | 18 |
| 61–65 | 7+16 | 7 | 2 | 2 | 13 | 40 | 24 | 10 | 4 | 5 | 36 | 19 | 8 | 17 |

gill rakers on the lower arch of the 1st gill arch in transitional specimens, but none on the upper arch. Epibranchial gill rakers were present in all juveniles examined (Table 4). The adult complement of 23–26 was present at about 50 mm.

An uninterrupted row of medial gill rakers is present on the 3d and 4th arches in 17-mm juveniles, but those on the 1st and 2d arches appear at 30–35 mm SL. There are 2 pseudobranchiae in the larva and transitional specimens. The number generally increased to 3 in juveniles of about 15 mm SL, and 6–7 in juveniles >45 mm SL.

**Dentition** The single larval specimen is toothless, but all transition specimens have teeth on the dentary, premaxillary, and basihyal, and, except for two individuals, on vomer and palatines as well (Table 3). Earliest appearances of maxillary, mid-dentary, and basibranchial teeth were in 16–17 mm juveniles. As in *H. latifrons*, there were more dentary than maxillary teeth in early stages; however, the number of maxillary teeth increased rapidly, becoming equal to that of the dentary by about 25 mm SL and more numerous after 35 mm (Table 4). Vomerine teeth numbered 2–5 and palatines 1–3 in the 16–50 mm SL range. In individuals 16 mm and larger, there were 3–12 teeth positioned around the perimeter of the basihyal, and 2–14 on the basibranchial. After a gradual increase, mid-dentary teeth numbered about 10 in individuals >50 mm SL. Mesopterygoid teeth appeared after 65 mm SL, and ectopterygoid teeth were found only in large adults.

**Photophores** The posterior gular organ ($GO_2$), subopercular organ (SBO), intraventral organ (IVO), and the orbital organ (OO) are the only photophores in individuals as large as 50 mm; they are covered over or lost in adults. The IVO photophore is located behind the yolksac (Fig. 2A). It becomes enclosed in a subconical, black pouch with a silvery, inner lining during the transitional period. The wider end of the pouch faces anteriorly and is covered by a transparent membrane. The photophore is located at the narrower, posterior end of the pouch, and is directed anteriorly. The other photophores are similarly housed in anteriorly facing, subconical pouches with a wider anterior opening and greater silvery surfaces.

Adult photophores face ventrally. Most begin appearing in juveniles. At 50–60 mm, the following organs begin to form: the jugular organ (JO) located between the bases of the pectoral fins; the thoracic organ (THO) behind the JO; the midventral organ (MVO) behind the THO and just before the pelvic fin bases; a pair of supraventral organs (SVO) just dorsal to the base of each pelvic fin; and the supra-anal organs (SAO) on both sides of the anus. The JO photophore first appears as one or more longitudinal bars (as in *H. latifrons*), but at about 65 mm begins to transform into a short transverse bar. Two more transverse bars, the THO and MVO, form behind the JO on the widely flattened ventral margin. Also appearing by 65 mm are several branchiostegal organs (BRO) on the branchiostegal rays, a postorbital organ (POO) just behind the eye, a pair of postanal organs (PAO) at about the middle of the anal fin, and an infracaudal organ (ICO) ventrally on the caudal peduncle. The anterior gular organ

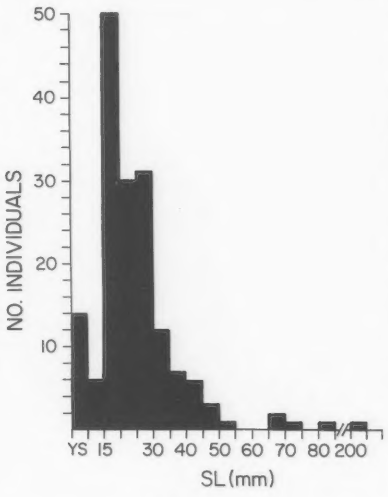


**Figure 3**
Length-frequency distribution of *Holtbyrnia latifrons* in SIO collections, 1950–73.

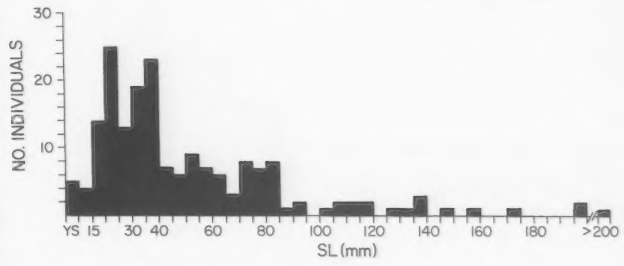


**Figure 4**
Length-frequency distribution of *Sagamichthys abei* in SIO collections, 1949–79.

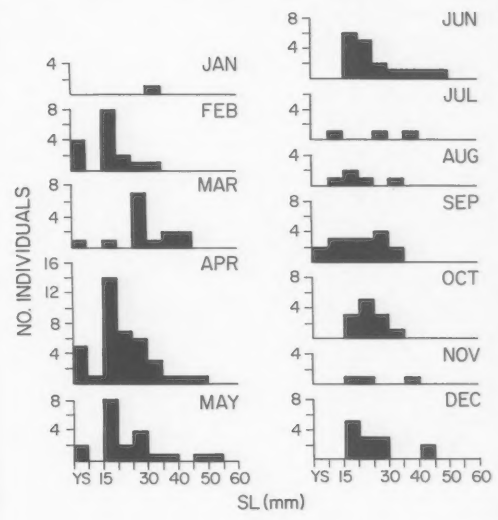


**Figure 5**
Length-frequency distribution of *Holtbyrnia latifrons* in SIO collections, 1950–73, presented by month of capture.

($GO_1$), located just behind the mandibular symphysis, and the pectoral organ (PO) on the pectoral fins, appear by 75 mm. The anal organ (AO), located just before the anus, appears in large adults.

**Remarks** Some young specimens of *H. latifrons* and *S. abei* with nearly exhausted yolksacs retain characteristics of the earliest stages, i.e., fragile mouth, short head, and toothless mouth. Only the fin rays are relatively well developed. They appear to be starved in spite of the presence of yolk material and may indicate that they need to feed while the yolk is present. The severely underdeveloped head and mouth indicate that development either lagged from the very early stages or had regressed from a more advanced stage. These larvae were assumed to be atypical, and were not included in the larval description.

## Distribution

In SIO samples, *H. latifrons* larger than 30 mm are rare and individuals >50 mm are nearly absent (Fig. 3); relatively small *H. latifrons* may avoid nets as large as a 3-m IKMT. Decline in size of *S. abei* in our samples is more gradual. The collection contains a number of individuals as large as 80 mm and a few even larger (Fig. 4). These results point to the inadequacy of nets as large as 3-m IKMT in sampling larger juveniles of both species.

The presence of individuals smaller than 20 mm during most of the year is interpreted as year-round spawning (Figs. 5, 6). These figures represent samples collected over many years pooled by month.

Depth distribution for both species is estimated to be 300–1000 m (Matsui and Rosenblatt 1987). On MLRG-SIO cruises, 63 opening-closing Leavitt net tows made in this depth zone collected 12 specimens of *H. latifrons* and 3 of *S. abei*. Fourteen net tows sampling shallower than 300 m and 30 tows sampling deeper than 1000 m on these cruises failed to catch

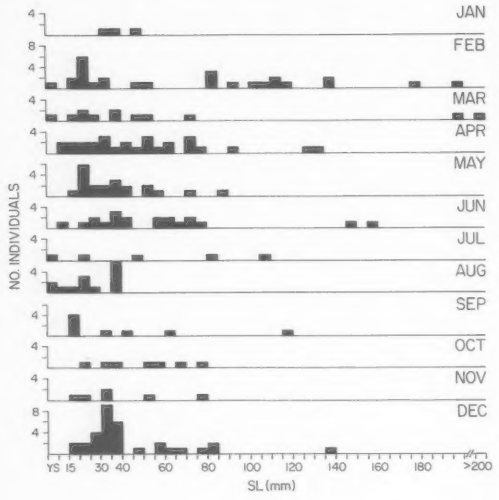


**Figure 6**
Length-frequency distribution of *Sagamichthys abei* in SIO collections, 1949–79, presented by month of capture.

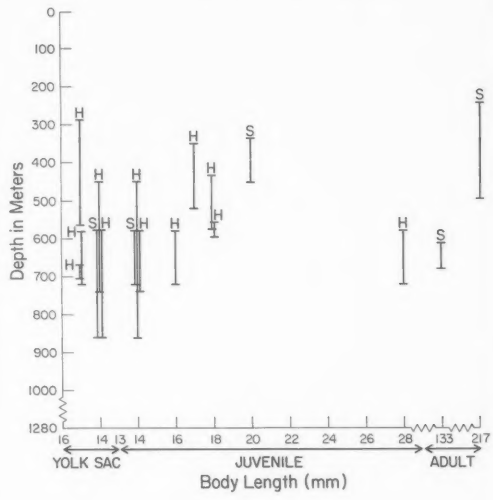


**Figure 7**
Sampling depths of opening-closing plankton net tows which captured *Holtbyrnia latifrons* (H) and *Sagamichthys abei* (S).

**Table 5**
Time and depth of capture of *Holtbyrnia latifrons* in opening-closing net tows. Asterisks = yolksac stage. Standard length (SL) in mm.

| SL | Date | Time | Depth (m) |
|---|---|---|---|
| *14 | 2/09/72 | 0921–1021 | 450–740 |
| *14 | " | " | " |
| 14 | " | " | " |
| *14 | 4/09/72 | 1146–1355 | 580–860 |
| 14 | " | " | " |
| *15 | 4/08/72 | 1639–1901 | 580–720 |
| 16 | " | " | " |
| 28 | " | " | " |
| *15 | 2/02/71 | 1745–1845 | 669–706 |
| 18 | " | " | 558–595 |
| 17 | 12/20/71 | 1748–1848 | 350–520 |
| 18 | 2/02/71 | 2320–0025 | 433–573 |
| *15 | 4/13/71 | 0013–0152 | 286–563 |

**Table 6**
Time and depth of capture of *Sagamichthys abei* in opening-closing nets. Standard length (SL) in mm.

| SL | Date | Time | Depth (m) |
|---|---|---|---|
| 20 | 2/09/72 | 0921–1021 | 333–450 |
| 14 | 4/08/72 | 1146–1355 | 580–860 |
| 133 | 11/04/69 | 1230–1300 | 615–680 |
| 15 | 4/08/72 | 1639–1901 | 580–720 |
| 213 | 3/28/70 | 2246–2350 | 250–500 |

either of these species. Samples of *H. latifrons* were from nets that had sampled depths of 290–860 m, and *S. abei* of 330–860 m (Fig. 7). All of these individuals were 20 mm and smaller, providing evidence that young stages occur over the entire depth range of the species. Large larval size and early appearance of presumed swimming and foraging capabilities, noted in this study, are apparent specializations for developing at these nutrient-poor depths.

Absence of day and night differences in depth of capture (Tables 5, 6) add to the previous evidence (Matsui and Rosenblatt 1987) suggesting the absence of diel migration in platytroctids. Hart (1973) and Fitch and Lavenberg (1968) mention the migration of young *S. abei* to within 200 m of the surface at night, but did not give the source of their information. However, records of platytroctids from depths 200 m and shallower are extremely rare and the single record from the Pacific Ocean may be an error (Matsui and Rosenblatt 1987).

Hydrographic data (Fig. 8) taken in an area where most Leavitt net tows were made show that samples represented in Figure 7 were taken below the thermocline at depths where the temperature range was ~4–8°C. CalCOFI (California Cooperative Oceanic

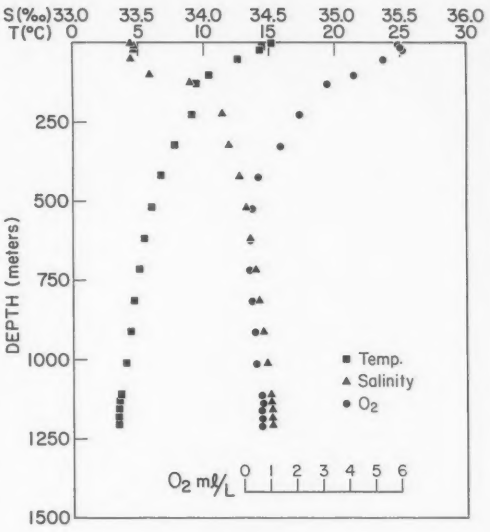


**Figure 8**

Temperature, oxygen, and salinity distribution at Station 7403G (32°32.4′N, 117°34.5′W), taken 27 March 1974 in the San Diego Trough.

Fisheries Investigation) station data from the area show seasonal changes in temperature below 300 m averaging less than 0.5°C (Lynn et al. 1982). Oxygen values of less than 1 mL/L occurred at these depths (Fig. 8). Gill filaments are highly developed (for platytroctids) in both species and are well adapted for this environment (Matsui and Rosenblatt 1987).

## Acknowledgments

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I thank Dr. Richard Rosenblatt for loan of specimens from the SIO Fish Collection, and his staff for curatorial assistance. I am grateful for advice received from Dr. Geoffrey Moser, and for his comments on an earlier draft; and to Barbara Sumida MacCall for useful comments on illustrations of the larvae and juveniles. Other figures were prepared by the Marine Life Research Illustration department. I wish to thank Ron McConnaughey for his able assistance during the MLRG cruises, and other participants too numerous to be named here.

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# Maturation, Spawning Seasonality, and Proximate Spawning Stimuli of Six Species of Tuna Baitfish in the Solomon Islands

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**Abstract.**– Length-at-sexual-maturity and spawning periodicity of the tuna baitfish *Encrasicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, *S. gracilis*, *S. lewisi*, and *Archamia zosterophora* were studied at two exploited fishing grounds and one unexploited site in the Solomon Islands. All species became sexually mature and capable of spawning at 70% of the largest size, except the apogonid *A. zosterophora* which matured at a larger size (80%). There was little site-related variability in length-at-first-spawning, although *S. lewisi* from Tulagi grew to a larger size and was larger than *S. lewisi* from other sites when it spawned for the first time. There was no evidence that length-at-first-spawning was affected by commercial baitfishing.

The timing and intensity of spawning of each species were extremely variable. All species spawned throughout the year, with one or two periods of more intense activity. The spawning peaks of the same species at different sites did not coincide, and no proximate stimuli correlated with spawning by any species at all sites. The timing of major spawning events was not random, nor did fish spawn as soon as they reached maturity. Spawning events at the three sites correlate with particular environmental conditions, especially moon phase and, less importantly, rainfall and temperature. These results are not consistent with the hypothesis that spawning is timed to maximize either local dispersal or the potential for larvae to find suitable food. Lack of clear proximate stimuli for spawning among the six species examined makes it difficult to predict the timing of major spawning events by these species.

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The pole-and-line fisheries for skipjack tuna *Katsuwonus pelamis* in the Pacific are dependent on adequate supplies of suitable bait. Engraulids (genus *Encrasicholina*) and dussumierids (genus *Spratelloides*) are the basis of the Solomon Islands tuna baitfishery, the largest in the region with catches of over 2000 t annually (Anon. 1988).

Knowledge of the reproductive biology of the main bait species may be important in developing management regimes to minimize the impact of the baitfishery on these species. Some aspects have been studied in the Solomon Islands (Evans and Nichols 1984) and elsewhere in the Pacific (Tester 1955; Tiews et al. 1971; Leary et al. 1975; Dalzell and Wankowski 1980; Conand 1985; Dalzell 1985, 1986, 1987ab; Lewis et al. 1983; McCarthy 1985; Clarke 1987) and in southeast Asia (Dharmamba 1960; Tham 1965; Luther 1979; Chen 1984, 1986). These studies suggest both genera spawn year-round, with periods of increased spawning during spring and summer (Leary et al. 1975, Tiews et al. 1971, Luther 1979) or with the change of monsoon (Dalzell and Wankowski 1980, Dalzell 1987b) or periods of high zooplankton production (Sitthichockpan 1972). However, timing of peak spawning is variable, both temporally (e.g., Dalzell 1987b) and between regions.

There have been several reviews (e.g., Scott 1979, Lam 1983, Bye 1984) of the importance of various cues which stimulate gonadal development and cause fish to spawn (proximate factors). Among temperate species, temperature and light are the most common cues (Scott 1979, Bye 1984). Other cues, such as food supply, moon phase, and rainfall, have also been suggested as important for spawning by tropical marine fishes (Johannes 1978, Lam 1983, Walsh 1987). However, the proximate stimuli that arouse increased spawning activity among baitfish remain obscure. Tester (1955) found that variations in egg production by *Encrasicholina purpureus* in Hawaii could not be adequately explained by temperature, salinity, or moon phase. Similarly, Muller (1976) showed that fluctuations in salinity and zooplankton biomass accounted for only 30% of the variation in egg production of *E. heterolobus* at Palau. Such poor correlations suggest that spawning may be random, or fish may begin to spawn as soon as they are physiologically capable of doing so.

The length at which *Encrasicholina* and *Spratelloides* become sexually mature appears to be variable both between and within countries of the southwestern Pacific (Dalzell and Wankowski 1980, Conand 1985, Dalzell 1985, McCarthy 1985, Dalzell 1987ab, Wright 1989), and these fish may adjust their life-history parameters to changes in their demography

or environment (Stearns and Crandall 1984). Such variability could have important implications for the baitfishing industry. Juveniles could be caught before they have had a chance to spawn, because the liftnets used in the baitfishery are not size-selective and catch all sizes of *Encrasicholina* and *Spratelloides* (see Evans and Nichols 1984).

The aims of this study were, first, to examine the length at maturity and the spawning seasonality of the six most abundant baitfish species (*Encrasicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, *S. lewisi*, *S. gracilis*, and the apogonid *Archamia zosterophora*); secondly, to determine whether spawning is random or correlated with environmental cycles; and, thirdly, to assess the effects, if any, of the commercial fishery on these reproductive parameters.

**Table 1**
Criteria used for staging female gonads of baitfish.

| Stage | Histology |
|---|---|
| (1) Immature | Oogonia present |
| (2) Developing/resting | Previtellogenic oocytes |
| (3) Maturing | Yolk precursor stage; some non-staining yolk |
| (4) Ripe | Non-staining yolk; developed chorion |
| (5) Running ripe | Homogeneous red-staining yolk; oocytes hydrated; development complete |
| (6) Spent | Atresion of ripe oocytes plus previtellogenic oocytes; presence of post-vitellogenic follicles |

## Methods and materials

### Sampling

Samples of six species of baitfish were collected from three sites each month for two years. Fish from commercial bait catches came from Munda and Tulagi, and fish from an unexploited control site came from Vona Vona, Solomon Islands. Sites and sampling methods are described in Milton et al (1990). Samples were usually collected between 2100 and 2200 hours. Two sites, Munda and Vona Vona, were in enclosed coral reef lagoons with little water movement and were approximately 20 km apart. The other site, Tulagi, consisted of a series of protected bays which opened into a narrow channel between two islands and was located over 300 km southeast of the other sites. Each month a random sample of over 100 fish of each species from each site was preserved in 4% formaldehyde and taken to the laboratory for analysis. On each sampling occasion, the water temperature, cloud cover, moon phase, and wind speed and direction were recorded. At least two 5-minute horizontal plankton tows ($\sim$100 $m^3$) were made with a 250-$\mu$mm mesh net (0.5 m diameter) 1 hour prior to fish collection. The daily rainfall at a village adjacent to each site was recorded throughout the study.

### Laboratory analyses

Fish were measured (standard length (SL) $\pm$ 0.5 mm) and weighed ($\pm$ 0.001 g) and the gonads were removed and weighed ($\pm$ 0.001 g). The gonads of up to 10 females of each species and of any other females with enlarged oocytes were randomly subsampled from each site sample each month. Gonads were embedded in paraffin wax, sectioned at 9 $\mu$m, and stained with Ehrlich's haemotoxylin and eosin (McManus and Mowry 1964). Gonad maturation stages were defined following Cyrus and Blaber (1984) and Hunter and Goldberg (1980). Each gonad was staged, based on the relative numbers of cells at each developmental stage (Young et al. 1987; Table 1), and the presence of any postovulatory follicles was noted. Gonosomatic indices (GSI) were calculated as the ratio of wet gonad weight to somatic weight (total weight minus gonad weight) expressed as a percentage.

Size-at-sexual-maturity was determined from the length at which a fish developed ripe eggs (Table 1: stage 4). Among fish that were only examined macroscopically, the criterion for sexual maturity was a gonosomatic index greater than the minimum GSI of fish that were shown histologically to have ripe eggs.

Fish examined histologically were considered to be in spawning condition if more than 85% of the eggs were fully hydrated, running-ripe (Table 1: late stage 5). The mean GSI $\pm$ 2 standard errors of these fish was calculated for each species at each site. The GSI value of the lower 95% confidence limit of the mean GSI of spawning fish was used as the indicator of spawning among fish examined macroscopically. The proportion in spawning condition in each sample was then calculated from the fraction of the sample (examined both histologically and macroscopically) with a GSI greater than this value. This criterion was used, as it was a conservative estimate of the real proportion spawning.

Plankton samples were split in half with a Folsom plankton splitter and one fraction was dried to a constant mass to provide an estimate of relative zooplankton biomass. The other fraction was sorted and the number of *Encrasicholina* eggs and larvae (Delsman 1931), the number of other eggs, larvae, and potential

prey (from those found by Milton et al. 1990) were counted. *Spratelloides* eggs are demersal (Leis and Trnski 1989) so were not sampled by this method.

### Data analyses

The proportion of each 1 mm length-class that were sexually mature was compared between sites. The normal approximation to the binomial distribution was used to estimate the 95% confidence limits of the proportion mature in any length-class. Confidence limits of the estimated proportion of the mature population spawning each month were calculated in a similar way.

To assess whether the timing of spawning was random, we calculated the proportion of the population spawning from the fraction of the entire sample of each species at each site during the study. This proportion was then compared with the proportion spawning each month. Monthly proportions greater than the 95% confidence limits to the normal approximation to a binomial distribution were scored as a plus sign. A nonparametric runs test (Sokal and Rohlf 1981) was used to test whether the distribution of plus signs was random.

The relationship between the proportion of fish in each monthly sample (of each species at each site) that were longer than the mean adult length at that site, and the proportion in that sample that were spawning, was examined using linear regression. A significant positive relationship between these proportions was used to assess whether fish spawned as soon as they were physiologically capable of doing so.

The relationships between possible proximate stimuli and the proportion spawning were compared by stepwise regression analysis. Variables that improved the fit were added to the model until the best three-variable model was obtained or the most significant fit was found. The proportion of each sample of each species in spawning condition was transformed by its arcsine square-root to reduce possible bias due to an excess of low values (Sokal and Rohlf 1981). The following 11 variables were compared for each species at each site: (1) sea-surface temperature, (2,3) prey biomass and density, (4) moon phase, (5) tide range, (6) cloud cover, (7) wind speed, and (8–11) rainfall between samples. Previous studies of spawning by these species (Dalzell 1985, 1987b) and other tropical inshore fishes (e.g., Johannes 1978, Walsh 1987) suggested that these variables may be important cues for these species. Initially, salinity and current speed were also measured, but as they varied little, they were not included in the analysis.

The variable moon phase was calculated by fitting a curve of the form $y = \sin(2\pi x) + \cos(2\pi x)$ where x = number of days since the last full moon prior to the start of sampling divided by 29.5 (days in a lunar month). This variable has higher values about the new and full moon. Rainfall data were regressed in several ways to assess the influence they may have on baitfish spawning: total rainfall since previous sample (usually 1 month)(Total); number of days since rain (Days); number of days since rain >25 mm (Days 25 mm); and number of days of rain since previous sample (Rain). Rainfall, cloud cover, and wind variables were transformed by their square root to normalize skewed values. Except for moon phase, positive relationships between the proportion of each species spawning and proximate variables are indicative of greater spawning activity at higher values.

To assess whether all variables were independent, proximate variables were correlated with one another. Principal component analysis (Sokal and Rohlf 1981) was also used to help identify variables that covaried within and between sites. A subset of proximate variables that behaved independently was identified and analysed separately. Where a potential stimulus had been measured in several ways (e.g., rainfall), the most biologically appropriate was chosen.

## Results

### Physical environment

The mean sea-surface temperature and monthly rainfall at each site varied seasonally during the sampling period (Figs. 1–3). The temperature ranged from 27.5° to 32.5°C at all sites, with lower temperatures during the dry season (May–September). Temperatures were lower in 1987 than 1988 at all sites. Rainfall occurred in all months at all sites. The amount of rainfall and its monthly distribution pattern were similar at the two closest sites, Munda and Vona Vona ($r^2$ 0.48, $P<$ 0.05), but Tulagi had a higher rainfall and different pattern of distribution.

### Maturation

A total of 1159 fish of six baitfish species from the three sites were examined histologically, including over 200 of each of the four most abundant species: *Encrasicholina devisi*, *E. heterolobus*, *Spratelloides delicatulus*, and *S. lewisi*.

***Encrasicholina*** Histological examination of ripe ovaries of *E. devisi* and *E. heterolobus* showed that almost all oocytes were in the most advanced stage of development, with a few at the yolk precursor stage (Table 1) or less developed. Although many females (~15%) of those examined had hydrated eggs, no post-vitellogenic follicles or spent fish (Stage 6) were observed.

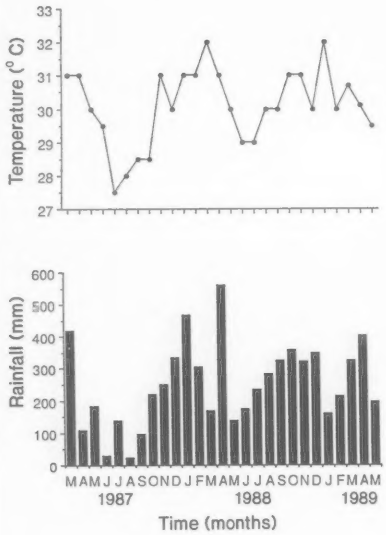


**Figure 1**
Mean monthly sea temperature and rainfall at Munda, Solomon Is., March 1987–May 1989.

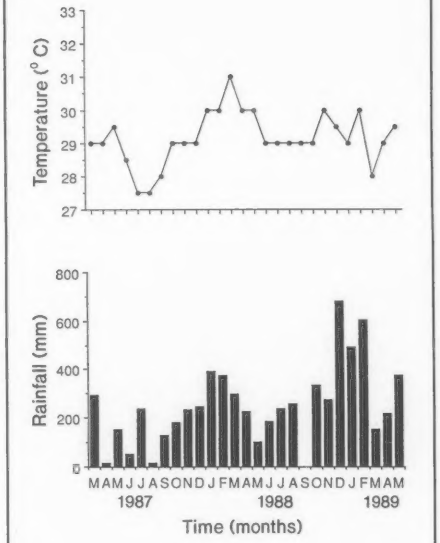


**Figure 3**
Mean monthly sea temperature and rainfall at Tulagi, Solomon Is., March 1987–May 1989.

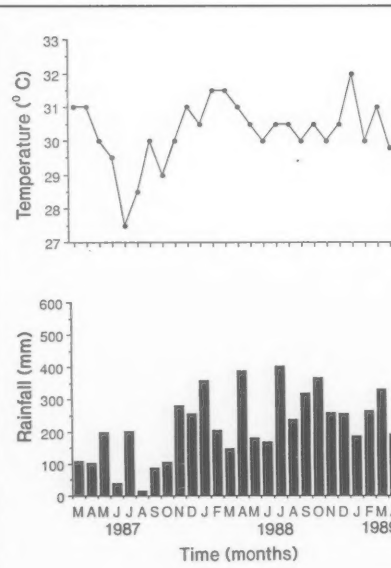


**Figure 2**
Mean monthly sea temperature and rainfall at Vona Vona, Solomon Is., March 1987–May 1989.

In both *Encrasicholina* species, fish with a GSI greater than 2% (Table 2) were sexually mature. The size at maturation of *E. devisi* was similar at all sites with 50% of the fish being sexually mature at 44–45 mm (Fig. 4a). At Munda and Vona Vona, fish beyond this length were capable of spawning, but at Tulagi the smallest *E. devisi* in spawning condition was 52 mm (Table 2). Sexual maturity in *E. heterolobus* was reached at approximately 43 mm at Munda and Vona Vona (Fig. 4b) and 45 mm at Tulagi. Hydrated eggs were not observed in *E. heterolobus* less than 50 mm, except at Munda where the smallest potential spawner was 45 mm (Table 2).

***Spratelloides*** The three *Spratelloides* species at the three sites were mature at similar lengths. *Spratelloides gracilis* and *S. lewisi* were sexually mature and had hydrated eggs at 35 mm (Table 2, Fig. 4c), except at Tulagi where the smallest *S. lewisi* with running ripe eggs was 40 mm. *Spratelloides delicatulus* reached sexual maturity at 37 mm (Fig. 4d), and running-ripe eggs were found in fish beyond this length. However, their length-at-maturity was not significantly different from the other *Spratelloides* species ($P>0.1$). For all species, a gonosomatic index of over 2% correlated with fish having ripe eggs (stage 4) in the ovary. Most oocytes in the ovaries of females of these species were at a

**Table 2**

Minimum gonosomatic index (GSI) values used as criteria to estimate proportion of sexually mature fish (stage 3) and proportion of fish spawning (late stage 5) at each site, and minimum size (SL, mm) of fish in spawning condition (based on values obtained from fish examined histologically). $N$ = sample size.

| | | Sexual maturity | | Spawning | | |
|---|---|---|---|---|---|---|
| Species | Site | GSI (%) | $N$ | GSI (%) | Length | $N$ |
| *Archamia zosterophora* | All | 2.5 | 57 | 3.8 | 37 | 23 |
| *Encrasicholina devisi* | Munda | 2.0 | 86 | 9.0 | 45 | 39 |
| | Vona Vona | 1.8 | 80 | 7.0 | 45 | 41 |
| | Tulagi | 1.8 | 58 | 5.7 | 52 | 11 |
| *Encrasicholina heterolobus* | Munda | 2.0 | 134 | 8.5 | 45 | 26 |
| | Vona Vona | 1.9 | 135 | 8.8 | 50 | 24 |
| | Tulagi | 1.6 | 84 | 10.0 | 51 | 31 |
| *Spratelloides delicatulus* | Munda | 2.0 | 60 | 5.7 | 37 | 34 |
| | Vona Vona | 1.0 | 35 | 5.9 | 37 | 23 |
| | Tulagi | 1.2 | 43 | 5.5 | 38 | 25 |
| *Spratelloides lewisi* | Munda | 1.5 | 235 | 13.3 | 35 | 210 |
| | Vona Vona | 2.8 | 107 | 11.2 | 35 | 90 |
| | Tulagi | 1.0 | 24 | 12.5 | 40 | 10 |
| *Spratelloides gracilis* | All | 2.0 | 12 | 11.9 | 35 | 6 |

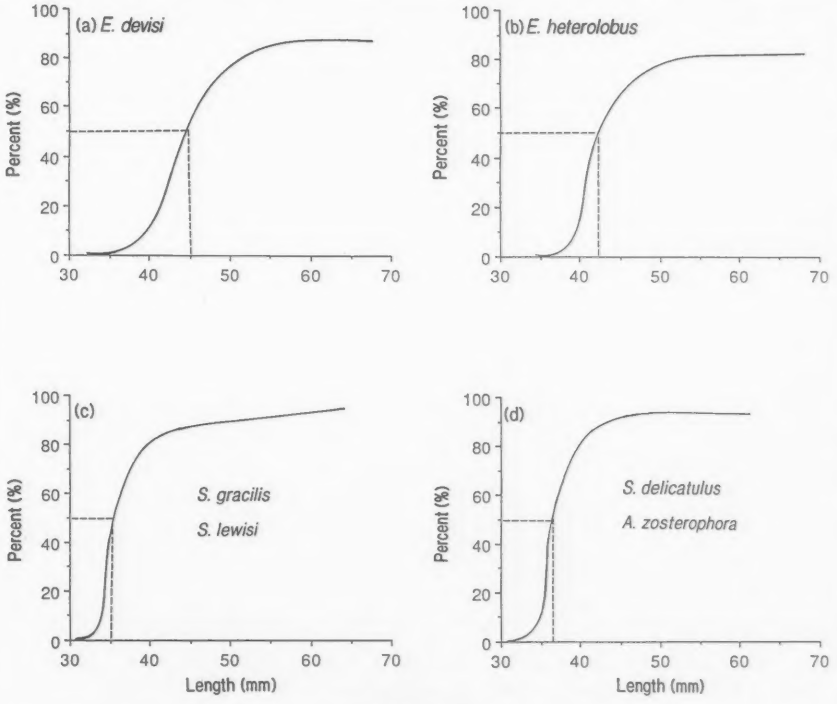


**Figure 4**

Logistic curves of best fit which describe the change in proportion of ripe eggs (stage 4) in the ovaries of six species of baitfish with increasing fish length.

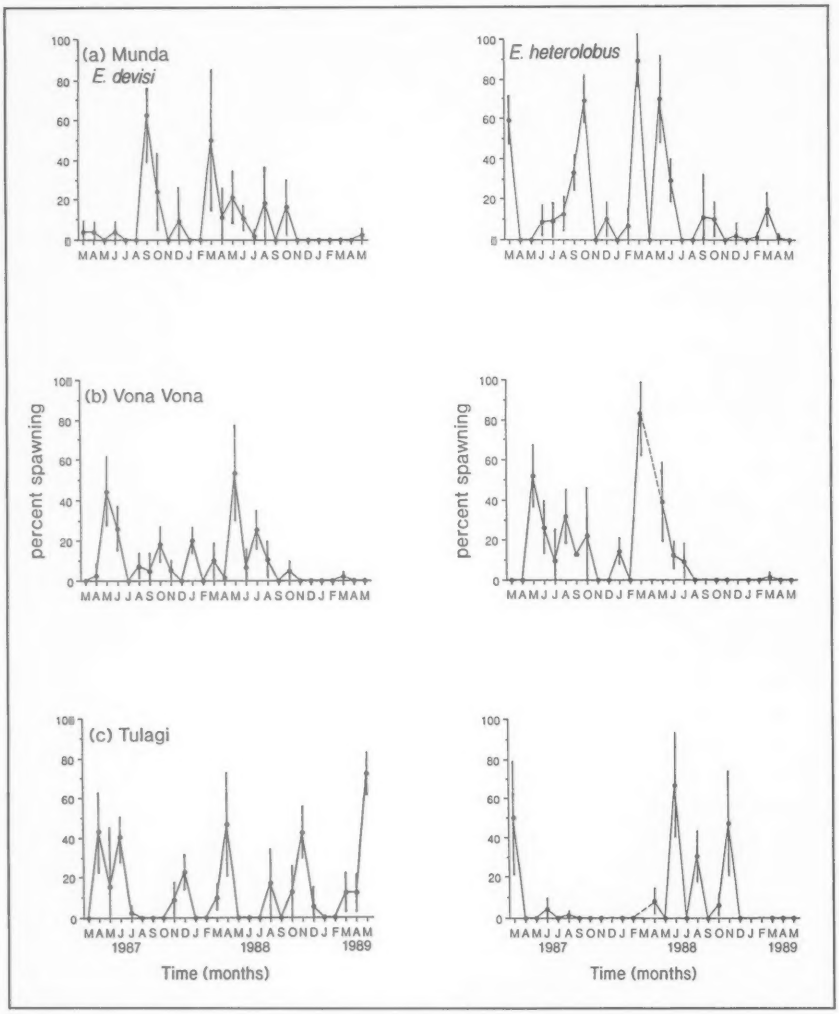


**Figure 5**
Monthly variation in proportion (± 95% confidence limits) of female *Encrasicholina devisi* and *E. heterolobus* spawning at three sites in the Solomon Islands, March 1987–May 1989.

similar stage of development. Fish with spent ovaries (Stage 6) were observed but were rare (<1%).

***Archamia zosterophora*** This species matured at 37 mm and was capable of spawning at this length (Table 2, Fig. 4d). A gonosomatic index value greater than 2.5% corresponded with sexual maturity (Table 2).

## Spawning seasons

All non-parametric tests showed a significant deviation from random spawning for all species at all sites ($P<0.05$). The distribution of deviations (plus signs) was either clumped or regular. For no species at any site were there significant positive correlations between the proportion of larger fish and the proportion spawning ($P>0.05$).

***Encrasicholina*** Spawning activity by the two *Encrasicholina* species showed both seasonal and interannual variation (Fig. 5). Both species had one or two major peaks in spawning each year. However, the pattern was different each year. Both species had a major peak in spawning activity early in the year (March–May) during 1987 and 1988, except for *E. devisi* at Munda in 1987 when most fish spawned later (Sept.–Oct.). The peak spawning was usually followed by several months when a small proportion of the population was spawning. Patterns of spawning at Munda and Vona Vona were more similar than at Tulagi. *Encrasicholina*

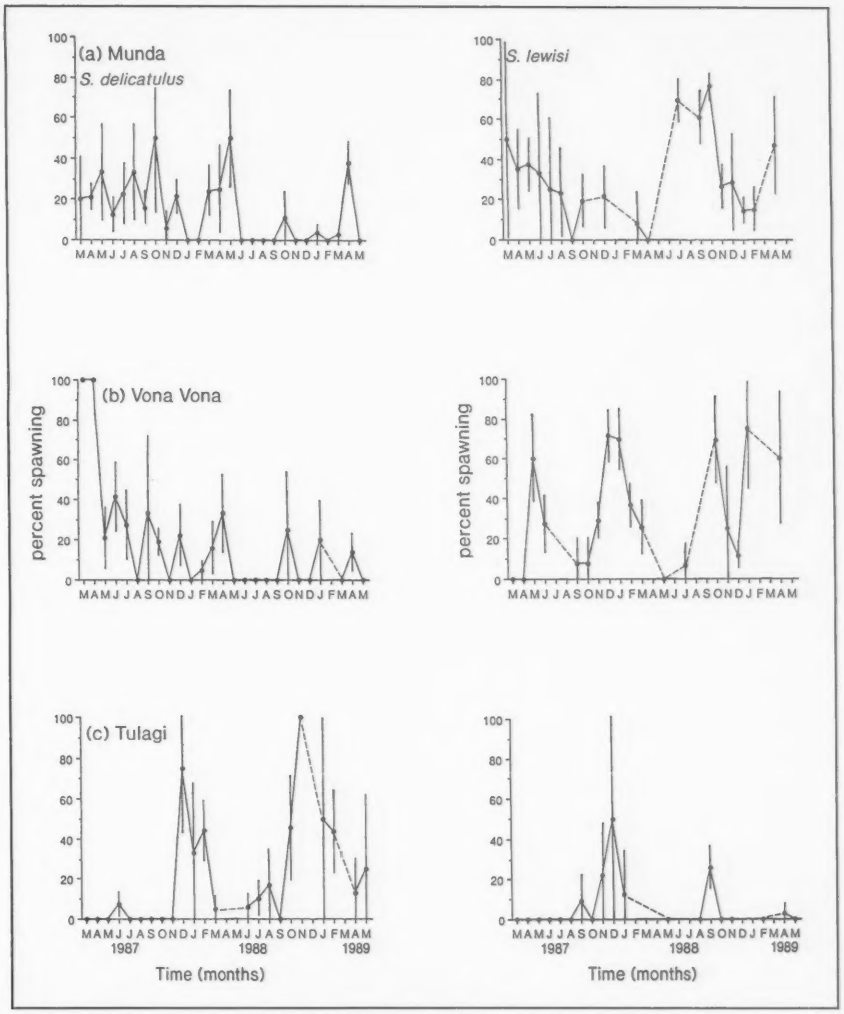
(a) Munda
S. delicatulus
S. lewisi
(b) Vona Vona
(c) Tulagi
percent spawning
M A M J J A S O N D J F M A M J J A S O N D J F M A M
1987
1988
1989
Time (months)

**Figure 6**
Monthly variation in proportion (± 95% confidence limits) of female *Spratelloides delicatulus* and *S. lewisi* spawning at three sites in the Solomon Islands, March 1987–May 1989.

*heterolobus* also had fewer, smaller peaks in spawning activity during most of 1987 at Tulagi and at all sites during the first five months of 1989. *Encrasicholina devisi* in Munda and Vona Vona did not have a March–May spawning peak in 1989.

***Spratelloides*** Two *Spratelloides* species also showed inter- and intraspecific differences in spawning activity between sites and between years (Fig. 6). *Spratelloides delicatulus* spawned continuously during 1987 at both Munda and Vona Vona, but the proportion spawning declined in the next 17 months. At Tulagi, the pattern was reversed, with less spawning during 1987 than in 1988–89 when there was a single major protracted spawning season from December to March (Fig. 6c). *Spratelloides lewisi* showed seasonal spawning activity at all sites. Fish from Vona Vona and Tulagi had a similar pattern during 1987–88, with increased spawning activity from October to May. However, the proportion spawning at Tulagi (50%) was much lower. The spawning activity of *S. lewisi* at Munda showed no seasonal increase during 1987, although during 1988 a higher proportion was spawning during the middle of the year (Fig. 6).

Too few *S. gracilis* and *A. zosterophora* could be obtained to determine their spawning seasons. However, a proportion of the fish sampled of both species was in spawning condition for several months of the year (Fig. 7). *Archamia zosterophora* data from Munda showed that some spawning activity occurred through-

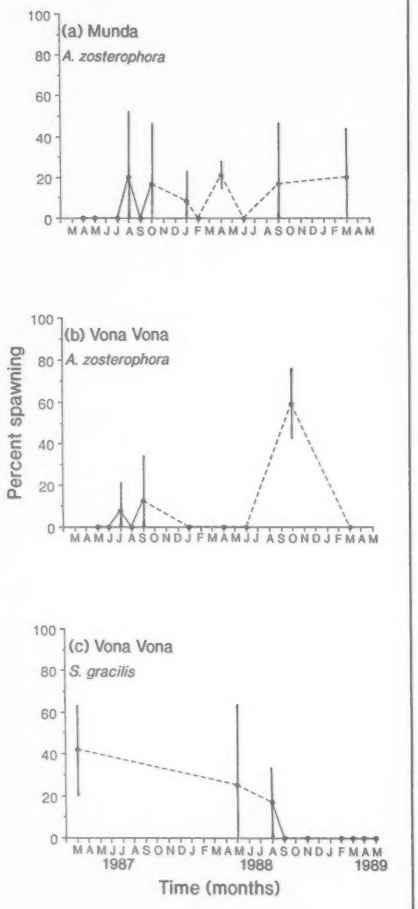
(a) Munda
A. zosterophora
(b) Vona Vona
A. zosterophora
(c) Vona Vona
S. gracilis
Percent spawning
M A M J J A S O N D J F M A M J J A S O N D J F M A M
1987
1988
1989
Time (months)

**Figure 7**
Monthly variation in proportion (± 95% confidence limits) of female *Archamia zosterophora* at Munda and Vona Vona (a, b), and female *Spratelloides gracilis* at Vona Vona (c), March 1987–May 1989.

out the year. At Vona Vona, however, there was a peak in spawning activity in samples taken in October 1988. The spawning data for *S. gracilis* are consistent with data for other *Spratelloides* at Vona Vona, with a decline in spawning activity during late 1988 and 1989 (Fig. 7).

**Eggs and larvae** *Encrasicholina* eggs were present in the zooplankton at each site most months of the sampling period (Fig. 8). The abundance of eggs did not vary greatly at each site during the period, although the samples from Vona Vona had fewer eggs than the other sites. Overall, the mean *Encrasicholina* egg density for the entire sampling period varied from $0.08 \pm 0.03/m^3$ at Vona Vona to $0.43 \pm 0.10$ at Munda. The overall mean teleost egg density was also lower at Vona Vona ($1.34 \pm 0.21/m^3$) and highest at Munda ($4.98 \pm /m^3$). *Encrasicholina* egg density did not correlate with total egg density at any site ($P>0.3$) or with the proportion of spawning *E. devisi* or *E. heterolobus* ($P>0.5$). No *Spratelloides* larvae were found, although apogonid larvae were present but could not be identified to species.

The density of *Encrasicholina* larvae followed a similar pattern at all sites (Fig. 8): larvae were present in most months, increasing every three or four months. In contrast to egg densities, *Encrasicholina* larvae reached higher densities at Vona Vona ($0.05 \pm 0.01/m^3$) than at Munda ($0.03 \pm 0.006/m^3$). Other fish larvae were also in higher densities at Vona Vona ($1.15 \pm 0.27$) than at the other sites (Munda $0.93 \pm 0.26$ and Tulagi $0.60 \pm 0.22$). The density of *Encrasicholina* larvae was significantly correlated with the density of other fish larvae at Munda ($r^2$ 0.62, $P<0.05$), but not at other sites.

## Proximate spawning stimuli

To assess the independence of the 11 proximate stimuli, all variables were correlated with one another (Table 3). At all sites, most measures of rainfall were significantly correlated ($P<0.05$). Total rainfall was negatively correlated with moon phase at Vona Vona and Tulagi, and with zooplankton biomass at Tulagi. Cloud cover was correlated with total rain and days of rain at Tulagi ($P<0.05$). Zooplankton biomass and density were correlated at Munda and Tulagi. However, there were no consistent correlations at all sites between non-rainfall variables (Table 3).

Principal component analysis was also performed separately on the proximate variables from each site. Rainfall variables at each site had loadings on the first three factors that were similar in magnitude and direction. Zooplankton density and biomass also covaried at each site. Temperature, moon phase, tide, and wind had loadings that varied independently for the first three factors at each site. These variables, zooplankton density, and the number of days of rain (which covaried least with other rainfall variables) were used in a separate stepwise regression analysis.

***Encrasicholina*** Analysis of the relationships between all 11 environmental parameters and the proportion of each sample spawning showed no consistent pattern for either species of *Encrasicholina* (Table 4). At Munda, spawning of *E. devisi* positively correlated

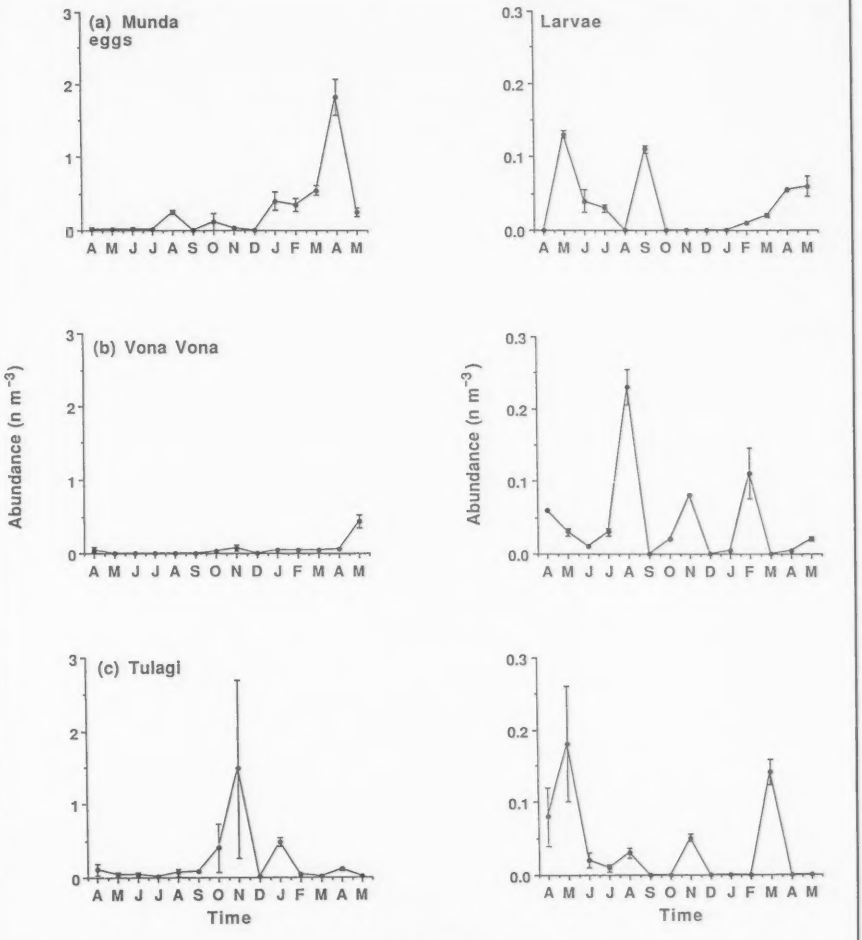


**Figure 8**

Variation in monthly abundance of *Encrasicholina* eggs and larvae (± range) at three sites in the Solomon Islands, April 1988–May 1989.

with wind and time since rain. At Vona Vona there was a negative correlation with wind strength and positive correlation with zooplankton biomass and tide range. Spawning at Tulagi correlated most strongly with time since heavy rainfall (>25 mm), temperature, and zooplankton biomass (Table 4). When all data were included, time since heavy rain was the only significant correlate.

Stepwise regression analysis of the six independent proximate stimuli (Table 5) showed a much poorer fit. The only site that showed a significant relationship was Vona Vona, where full moon, greater tidal range, and low wind accounted for 40% of the variation in spawning of *E. devisi*. Although not significant, days of rain had a similar coefficient in the equations of best fit at both Munda and Tulagi (Table 5), which suggests that rainfall had a similar effect on spawning at these sites.

The significant proximate stimuli for *E. heterolobus* differed between sites (Table 4). The best fit was obtained at Vona Vona ($r^2$ 0.44, $P<0.01$) where greater spawning occurred when cloud cover was low and moon phase approached full. Spawning was negatively related to total rainfall and days since rain at Munda ($r^2$ 0.3, $P<0.05$), and there was a negative

**Table 3**

Correlations between independent environmental variables. *$P<0.05$. See "Data analyses" section for explanation of variables.

| Variable | Temp. | Biomass | Density | Moon phase | Tide range | Cloud cover | Wind speed | Rain* Total | Rain* Days | Rain* Days 25mm | Rain* Rain |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Munda** | | | | | | | | | | | |
| Temperature | x | −0.02 | −0.12 | −0.32 | −0.20 | 0.41 | 0.18 | 0.46* | 0.04 | −0.19 | 0.37 |
| Biomass | | x | 0.73* | −0.21 | −0.08 | 0.21 | −0.38 | 0.08 | −0.36 | 0.00 | 0.30 |
| Density | | | x | 0.05 | 0.23 | 0.29 | −0.23 | −0.03 | −0.22 | 0.05 | −0.01 |
| Moon phase | | | | x | 0.06 | 0.01 | 0.50* | −0.29 | 0.3 | 0.51* | −0.29 |
| Tide range | | | | | x | −0.07 | 0.07 | −0.09 | 0.47* | 0.12 | −0.05 |
| Cloud cover | | | | | | x | 0.25 | 0.30 | 0.01 | 0.11 | 0.17 |
| Wind speed | | | | | | | x | 0.16 | 0.33 | 0.23 | −0.11 |
| Total* | | | | | | | | x | −0.21 | −0.62* | 0.69* |
| Days | | | | | | | | | x | 0.52* | −0.31 |
| Days 25mm | | | | | | | | | | x | −0.54* |
| Rain | | | | | | | | | | | x |
| **Vona Vona** | | | | | | | | | | | |
| Temperature | x | −0.05 | −0.46* | −0.25 | 0.08 | 0.38 | 0.06 | 0.25 | −0.19 | 0.10 | 0.24 |
| Biomass | | x | 0.31 | −0.03 | −0.32 | 0.21 | 0.39 | −0.09 | −0.15 | −0.41 | 0.08 |
| Density | | | x | 0.19 | −0.27 | −0.15 | 0.26 | −0.19 | −0.03 | −0.25 | 0.04 |
| Moon phase | | | | x | 0.08 | −0.29 | −0.09 | −0.55* | 0.26 | 0.42* | −0.36 |
| Tide range | | | | | x | −0.05 | −0.34 | −0.30 | 0.28 | 0.46* | −0.34 |
| Cloud cover | | | | | | x | 0.49* | 0.10 | −0.21 | 0.03 | 0.25 |
| Wind speed | | | | | | | x | 0.16 | −0.06 | −0.28 | 0.12 |
| Total* | | | | | | | | x | −0.49* | −0.56* | 0.62* |
| Days | | | | | | | | | x | 0.33 | −0.83* |
| Days 25mm | | | | | | | | | | x | −0.44* |
| Rain | | | | | | | | | | | x |
| **Tulagi** | | | | | | | | | | | |
| Temperature | x | −0.22 | −0.20 | −0.22 | −0.33 | 0.10 | −0.11 | 0.33 | −0.40 | −0.21 | 0.11 |
| Biomass | | x | 0.70* | 0.41* | 0.24 | −0.33 | −0.15 | −0.45* | 0.14 | 0.09 | −0.44* |
| Density | | | x | 0.19 | 0.22 | −0.45* | −0.45* | −0.40* | 0.49 | −0.05 | −0.52* |
| Moon phase | | | | x | 0.22 | −0.38 | 0.04 | −0.51* | −0.00 | 0.10 | −0.35 |
| Tide range | | | | | x | −0.18 | −0.19 | −0.18 | 0.28 | −0.13 | −0.26 |
| Cloud cover | | | | | | x | 0.39 | 0.52* | −0.33 | −0.25 | 0.72* |
| Wind speed | | | | | | | x | 0.06 | −0.24 | 0.10 | 0.21 |
| Total* | | | | | | | | x | −0.36 | −0.42* | 0.67* |
| Days | | | | | | | | | x | 0.15 | −0.44* |
| Days 25mm | | | | | | | | | | x | −0.29 |
| Rain | | | | | | | | | | | x |

*Total = Total rainfall since previous sample
Days = No. days since rain
Days 25mm = No. days since rain >25mm
Rain = No. days of rain since previous sample.

relationship with tide range at Tulagi. Overall, the most significant variable was total rainfall. The results of the regression analysis of the independent stimuli (Table 5) were similar, except at Vona Vona where a four-variable model including zooplankton density, wind, and days of rain gave the best fit.

***Spratelloides*** For *S. delicatulus*, moon phase was highly correlated with spawning and accounted for at least 26% of the variation in spawning periodicity at all sites (Table 4). Increased cloud cover and reduced tidal range were also correlated with spawning at Vona Vona and Tulagi. However, when data from all sites were combined, the most significant correlates were

**Table 4**

Stepwise multiple regresssion of best fit of 11 proximate variables related to the proportion of each species spawning at each site. Maximum number of variables allowed was three. Negative sign preceding a variable indicates negative correlation; $r_p^2$ = partial correlation coefficient, $r^2$ = overall correlation coefficient, $P$ = significance level, $N$ = sample size.

| Species | Site | | Environmental parameter | $r_p^2$ | $r^2$ | $P$ | $N$ |
|---|---|---|---|---|---|---|---|
| *Encrasicholina devisi* | Munda | | Days since 25 mm rain | 0.16 | 0.35 | <0.05 | 22 |
| | | – | Days since rain | 0.10 | | | |
| | | | Wind speed | 0.09 | | | |
| | Vona Vona | – | Wind speed | 0.33 | 0.50 | <0.01 | 21 |
| | | | Zooplankton biomass | 0.11 | | | |
| | | | Tide range | 0.06 | | | |
| | Tulagi | | Days since 25 mm rain | 0.31 | 0.59 | <0.005 | 19 |
| | | | Temperature | 0.25 | | | |
| | | | Zooplankton biomass | 0.03 | | | |
| | Overall | | Days since 25 mm rain | 0.12 | 0.14 | <0.01 | 62 |
| | | – | Days since rain | 0.02 | | | |
| *Encrasicholina heterolobus* | Munda | – | Total rainfall | 0.19 | 0.30 | <0.05 | 22 |
| | | – | Days since rain | 0.11 | | | |
| | Vona Vona | – | Cloud cover | 0.32 | 0.44 | <0.01 | 21 |
| | | | Moon phase | 0.12 | | | |
| | Tulagi | – | Tide range | 0.24 | 0.24 | <0.05 | 16 |
| | Overall | – | Total rainfall | 0.11 | 0.14 | <0.05 | 59 |
| | | | Temperature | 0.03 | | | |
| *Spratelloides delicatulus* | Munda | | Moon phase | 0.28 | 0.28 | <0.01 | 22 |
| | Vona Vona | | Moon phase | 0.26 | 0.50 | <0.01 | 22 |
| | | – | Tide range | 0.13 | | | |
| | | | Cloud cover | 0.11 | | | |
| | Tulagi | | Moon phase | 0.51 | 0.60 | <0.005 | 17 |
| | | | Cloud cover | 0.09 | | | |
| | Overall | – | Tide range | 0.05 | 0.13 | <0.05 | 61 |
| | | – | Zooplankton biomass | 0.04 | | | |
| | | | Cloud cover | 0.04 | | | |
| *Spratelloides lewisi* | Munda | | Zooplankton biomass | 0.22 | 0.41 | <0.05 | 18 |
| | | | Days since rain | 0.10 | | | |
| | | | Cloud cover | 0.09 | | | |
| | Vona Vona | | Cloud cover | 0.29 | 0.62 | <0.01 | 15 |
| | | – | Wind speed | 0.19 | | | |
| | | – | Moon phase | 0.14 | | | |
| | Tulagi | – | Temperature | 0.39 | 0.66 | <0.01 | 14 |
| | | – | Zooplankton biomass | 0.16 | | | |
| | | – | Days since rain | 0.11 | | | |
| | Overall | | Temperature | 0.13 | 0.20 | <0.01 | 47 |
| | | | Zooplankton biomass | 0.07 | | | |
| *Spratelloides gracilis* | Vona Vona | | Moon phase | 0.62 | 0.82 | <0.05 | 8 |
| | | | Temperature | 0.10 | | | |
| | | | Zooplankton biomass | 0.10 | | | |
| *Archamia zosterophora* | Munda | – | Days since 25 mm rain | 0.49 | 0.65 | <0.01 | 11 |
| | | – | Days since rain | 0.16 | | | |
| | Vona Vona | | Zooplankton biomass | 0.42 | 0.42 | <0.05 | 10 |
| | Overall | – | Days since 25 mm rain | 0.30 | 0.41 | <0.05 | 21 |
| | | | Zooplankton biomass | 0.11 | | | |

negative tide range, cloud cover, and negative zooplankton biomass. When the number of variables were reduced (Table 5), wind and days of rain at Vona Vona and temperature at Tulagi were also significant ($P<0.05$). Among samples from months where spawning had been detected, moon phase and days of rain showed the best fit.

There was significant positive correlation between spawning of *S. lewisi* and zooplankton biomass and days since rain at Munda (Table 4). Lower temperature,

**Table 5**

Stepwise linear regression models of best fit for six independent proximate stimuli. y = percent spawning; t = temperature; d = zooplankton density; m = moon phase; ti = tidal range; w = wind speed; r = days of rain between samples; $r^2$ = multiple regression coefficient; $P$ = significance level; $N$ = sample size. Overall includes all samples; spawning includes only months when spawning was detected.

| Species | Site | Model | $r^2$ | $P$ | $N$ |
|---|---|---|---|---|---|
| *Encrasicholina devisi* | Munda | y = 0.53 − 0.02r | 0.14 | <0.08 | 22 |
| | Vona Vona | y = 3480m + 0.29ti − 0.15w − 3479 | 0.40 | <0.05 | 21 |
| | Tulagi | y = 0.14t − 0.0003d − 0.18r − 2.89 | 0.33 | <0.07 | 19 |
| | Spawning | y = 0.52 − 0.006r | 0.02 | <0.44 | 40 |
| | Overall | y = 0.50 − 0.0001d − 0.01r | 0.07 | <0.10 | 62 |
| *Encrasicholina heterolobus* | Munda | y = 0.92 − 0.15r | 0.08 | <0.22 | 22 |
| | Vona Vona | y = 3741m + 0.0001d − 0.26w − 0.08r − 3742 | 0.50 | <0.05 | 21 |
| | Tulagi | y = 0.79 − 0.92ti | 0.24 | <0.05 | 16 |
| | Spawning | y = 0.10t − 0.57ti − 0.02r − 1.73 | 0.27 | <0.05 | 33 |
| | Overall | y = 2459m − 0.42ti − 0.02w − 0.01r − 2458 | 0.16 | <0.05 | 59 |
| *Spratelloides delicatulus* | Munda | y = 7084m − 0.0001d − 0.37ti − 7083 | 0.38 | <0.05 | 22 |
| | Vona Vona | y = 10759m + 0.27w + 0.13r − 10759 | 0.49 | <0.01 | 22 |
| | Tulagi | y = 8825 + 0.11t − 8828m | 0.51 | <0.005 | 17 |
| | Spawning | y = 3510m + 0.02r − 3510 | 0.16 | <0.05 | 38 |
| | Overall | y = 0.57 − 0.36ti | 0.05 | <0.11 | 61 |
| *Spratelloides lewisi* | Munda | y = 0.0003d + 0.17r − 0.39 | 0.24 | <0.13 | 18 |
| | Vona Vona | y = 5217 − 5216m | 0.15 | <0.15 | 15 |
| | Tulagi | y = 1.40 − 0.04t − 0.25ti | 0.26 | <0.17 | 14 |
| | Spawning | y = 0.02r − 0.0001d + 0.34 | 0.30 | <0.01 | 29 |
| | Overall | y = 0.08t − 0.03w + 0.01r − 2.34 | 0.23 | <0.01 | 47 |
| *Spratelloides gracilis* | Vona Vona | y = 12588m + 0.56ti − 12587 | 0.86 | <0.05 | 8 |
| *Archamia zosterophora* | Munda | y = 4262 − 4262m − 0.49ti | 0.50 | <0.06 | 11 |
| | Vona Vona | y = 0.08t − 1.98ti − 0.80 | 0.94 | <0.001 | 10 |
| | Spawning | y = 3957 − 3956m | 0.30 | <0.16 | 8 |
| | Overall | y = 0.72 − 0.79ti | 0.46 | <0.001 | 21 |

low zooplankton biomass, and recent rain explained 66% of the variation in spawning periodicity at Tulagi ($P<0.01$). Cloudy conditions, light winds, and waning moon phases were the variables most correlated with spawning in *S. lewisi* at Vona Vona (Table 4). However, the combined data showed that temperature and zooplankton biomass were the most significant stimuli. These conflicting results were reflected in the second analysis, where the stimuli chosen could not explain a significant amount of the variation in spawning at any site (Table 5).

Correlations between environmental stimuli and the spawning periodicity of *S. gracilis* could only be analysed for fish from Vona Vona. Most variation could be explained by moon phase, temperature, tide, and zooplankton biomass (Tables 4, 5). Most fish spawned at full moon and when temperature, tidal range, and prey biomass were high.

***Archamia zosterophora*** This species was most frequently caught at Munda and Vona Vona where it spawned most often during periods of high rainfall (at Munda), and when zooplankton biomass was high (at Vona Vona) (Table 4). These variables were also the most significant when all data were combined. When these variables were excluded from the analysis (Table 5), lower tidal range and higher temperatures (Vona Vona) were the only significant stimuli.

## Discussion

Size-at-sexual-maturity of some *Encrasicholina* and *Spratelloides* species from the Solomon Islands varied both locally and compared with other studies elsewhere in the South Pacific.

*Encrasicholina heterolobus* and *S. gracilis* reached sexual maturity at smaller lengths than previously reported (Tham 1965; Tiews et al. 1971; Dalzell and Wankowski 1980; Conand 1985; Dalzell 1985, 1987b). Such differences may be partly an artifact of the different sexual maturity criteria used. The present study,

unlike others, used histological examination of gonads to verify macroscopic stages.

In the Solomon Islands, *Encrasicholina devisi* reached sexual maturity at 45 mm, and some fish at this size were in spawning condition. This is consistent with results from Papua New Guinea (Dalzell and Wankowski 1980), New Caledonia (Conand 1985), and southern India (Luther 1979). *Spratelloides delicatulus* also showed little difference throughout the region in length-at-sexual-maturity (Lewis et al. 1983, Conand 1985, McCarthy 1985).

*Spratelloides lewisi* showed local variation in length-at-sexual-maturity. Fish from Tulagi were not sexually mature at less than 40 mm (compared with 35 mm at other sites) and they also grew to a greater size than fish from the other sites (unpubl. data).

Length-at-first-spawning, however, was similar for both *Encrasicholina* species and *S. delicatulus* throughout the region (Dalzell and Wankowski 1980, Lewis et al. 1983, Conand 1985), except for *E. heterolobus* at Munda, where fish were in spawning condition at a smaller length than at the other sites in the Solomon Islands.

Both *Spratelloides lewisi* and *S. gracilis* showed variation in length-at-first-spawning between sites. At Tulagi, *S. lewisi* did not spawn until a much greater length was attained. These results are consistent with those of Dalzell (1987), who found a difference of 9 mm in the length-at-first-spawning in two populations of *S. lewisi* in Papua New Guinea waters. Dalzell (1985) also found that Papua New Guinea *S. gracilis* did not develop ripe eggs until 44 mm, which was much larger than the length-at-first-spawning of fish from the Solomon Islands (35 mm). Unfavorable conditions for reproduction may delay the onset of gonadal development in these species at some sites to help offset reproductive uncertainty (Mann and Mills 1979).

No comparative data on length-at-sexual-maturity of *A. zosterophora* are available, and there are few data for other similar-sized apogonids. However, this species matures at almost 80% of maximum size, which is larger than in the clupeoids (70%). The subtropical Australian species *Apogon fasciatus* also matures at about 70% of maximum size (90 mm) near Brisbane (K. Warburton, Zool. Dep., Univ. Queensland, Brisbane, Australia, unpubl. data).

The relationship between length-at-first-spawning and maximum length of the Solomon Islands baitfish closely fits that found for other clupeoids (Beverton 1963). Beverton (1963) showed that length-at-first-spawning among clupeoids is closely proportional to maximum length, with smaller species spawning at a smaller size (relative to their maximum) than larger ones (Blaxter and Hunter 1982). Longhurst and Pauly (1987) hypothesize that length-at-sexual-maturity and maximum length are determined by the interactions of oxygen supply and demand. Any species of fish living in cold water should grow to a greater size and mature at a larger size than the same species in warm water, given similar food supplies. Water temperature at Tulagi was consistently 1–2°C colder than at the other sites, and this may account for differences in these parameters in *S. lewisi* at this site. The regional differences seen in *E. heterolobus* and *S. gracilis* also support this idea, with fish from higher latitudes maturing at greater lengths. However, similar patterns were not found in the other species. Availability of food also must play an important role by affecting growth rates.

Many clupeoids, including most engraulids, are multiple spawners (Blaxter and Hunter 1982), and studies of other engraulids suggest they spawn batches of eggs every 2–10 days (Hunter and Goldberg 1980, Alheit et al. 1984, Clarke 1987). Smaller species (e.g., *Encrasicholina purpureus*) spawn more frequently during the peak spawning period (as often as every 2 days; Clarke 1987). The spawning frequency of multiple spawning fish can be determined by the presence or absence of postvitellogenic follicles in the ovaries; their presence indicates that a fish has spawned within the previous 24–48 hours (Hunter and Goldberg 1980). Clarke (1987) reported that postvitellogenic follicles were distinguishable in *Encrasicholina purpureus* up to 16 hours after spawning. In our study, we did not find either postvitellogenic follicles or a continuous egg-size distribution indicative of multiple spawning (Blaxter and Hunter 1982). However, the similarity in reproductive behavior of *Encrasicholina* species and the presence of eggs in the plankton throughout most of the year suggest that *E. devisi* and *E. heterolobus* are also multiple spawners. Our data on *Encrasicholina devisi* and *E. heterolobus* were consistent with that of Leary et al. (1975) on *Encrasicholina purpureus*. We found, as had Leary et al., only two egg sizes: one advanced and one with all eggs at the yolk-precursor stage of development. Leary et al. (1975) interpreted these results to indicate that *E. purpureus* spawned once in its lifetime. However, Clarke (1987) found that *E. purpureus* eggs could mature very rapidly, and hence timing of sampling was critical. Running-ripe eggs were only present shortly before spawning, which occurred one or two hours after sunset. If *E. devisi* and *E. heterolobus* are batch spawners similar to *E. purpureus*, then we would expect to collect only fish about to spawn in our samples, as the postvitellogenic follicles of fish that spawned the previous night would have degraded (Clarke 1987). However, spawning is probably less frequent than in the smaller *E. purpureus* because greater energy is required by larger fish to maintain continuous spawning (Hunter and Leong 1981).

Ovaries of the three species of *Spratelloides* and *A. zosterophora* all contained only a single size-group of developing oocytes, which suggests that they spawn all the eggs in the ovaries at once. Whether a female develops another batch of eggs after spawning was not determined. However, given the high proportion of female *Spratelloides* spawning at any time, it seems probable that each female produces more than one batch of eggs. Most apogonids are mouth-brooders (Thresher 1984), and other species have been found with eggs in their buccal cavity that are at more than one stage of development, which suggests that they are multiple spawners (Thresher 1982).

Flexibility in reproduction is well documented among a range of animals and usually involves a direct physiological response to nutrient level or some associated environmental cue (Giesel 1976). Extended breeding seasons are a common phenomenon among tropical fishes, particularly coral reef fish (Munro et al. 1973, Russell et al. 1977, Johannes 1978, Lowe-McConnell 1979, Walsh 1987). The present work, and other studies of *Encrasicholina*, *Spratelloides*, and apogonid reproduction (Leary et al. 1975; Russell et al. 1977; Dalzell and Wankowski 1980; Dalzell 1985, 1987ab; Conand 1985; McCarthy 1985; Clarke 1987), found that the spawning season of these fish is protracted, with some individuals in the population spawning at any time during the year. There are also periods when most of the population is spawning. If reproduction were controlled only by endogenous cycles and females spawned as soon as they were physiologically capable, then as the proportion of larger fish increased there should be a greater proportion of spawning fish in the population. Examination of our data failed to find any significant relationship between the proportion of larger fish and the proportion spawning for any species at any site. Non-parametric tests also showed that the frequency of major spawnings was not random. Hence it is unlikely that spawning periodicities shown by baitfish are a result of intrinsic mechanisms. The timing and intensity of periods of increased spawning activity appear to be highly variable, linked to exogenous stimuli and with no endogenous rhythms.

Of the several hypotheses put forward to explain the timing of fish reproduction, one of the more widely accepted is the "match-mismatch" hypothesis of Cushing (1967). This proposes that if the timing of reproduction coincides with peaks in the plankton cycle, larval survival is enhanced. Timing of peak plankton production does not necessarily occur at exactly the same time each year, so if fish are serial spawners they can exploit the plankton cycle well (e.g., California sardine) by spawning during any of the months of spring or summer when food becomes superabundant (Cushing 1975). Much of the data to support this hypothesis comes from temperate waters, but data on the reproduction of tropical clupeoids from open oceans also support this hypothesis (Longhurst 1971, Roy et al. 1989).

Johannes (1978) proposed that coastal tropical fish tend to spawn at times and locations that will reduce predation on larvae by transporting them out of the adult habitat, while enabling them to return to suitable areas for postlarval settlement. At many sites, periods of major spawning coincide with low winds and full moon. The baitfish species studied here spawn in lagoons fringed by coral reefs, where water currents are negligible. Both adults and larvae are pelagic and live in the deeper waters of the lagoon. When the larvae are abundant, adults prey on them (Milton et al. 1990). If deeper waters of the lagoon are the favored habitat, then according to Johannes' hypothesis (1978) adults should spawn when local flushing is greatest (spring tides) but regional flushing is least (low winds) to ensure larvae develop in the same area.

Although baitfish spawn throughout the year, with no consistent seasonal pattern, there appears to be some regularity in their spawning. At each site, certain proximate factors were significant for more than one species. This suggests that if these fish are responding to exogenous spawning stimuli, their influence must be interposed by local hydrography and topography. At Vona Vona, spawning by five of the six species examined was correlated with moon phase. Both *Encrasicholina* and two *Spratelloides* species spawned around the full moon, while *S. lewisi* spawned around the new moon. Both *Encrasicholina* species also spawned when wind strength was reduced. The spawning around phases of the moon has often been assumed to be related to increased tidal exchange during spring tides (e.g., Johannes 1978, Walsh 1987). However, in this study greater tidal range at any site was not directly correlated with moon phase (Table 3). Vona Vona is an enclosed lagoon with many islands and patch reefs. In this habitat, spawning around the full or new moon does not appear to be related to the potential to flush eggs and larvae to more favorable habitats by tidal water movement (Johannes 1978). Possibly, spawning around the full moon when the wind is reduced may increase spawning success by increasing visibility at night (during spawning) and reducing the dispersal of eggs, and hence increasing the chances of fertilization. This hypothesis would also explain the strong negative relationship between spawning by *A. zosterophora* and tidal range at this site.

Moon phase was the single variable most often correlated with spawning in this study, both for five species at one site (Vona Vona) and for one species at different sites (*S. delicatulus*). However, our data do not indicate a strong relationship with moon phase for either *Encrasicholina* species at Munda or Tulagi. This

suggests that either local conditions exert a strong influence on the timing of reproduction in these species or that at these sites reproduction is not strongly linked to particular environmental events. Wright (1989) also found no relationship between spawning by *E. heterolobus* in Indonesia and temperature, rainfall, or tidal phase, and suggested that these factors were not influencing spawning.

However, among the other species, temperature and reduced tidal range appear to be more important at Tulagi. Higher temperatures should allow increased growth under favorable conditions, and reduced tidal exchange would reduce egg movement away from favorable habitats.

While rainfall has been suggested as a proximate factor influencing spawning by *Encrasicholina* species in Papua New Guinea (Dalzell and Wankowski 1980; Dalzell 1984, 1987b), in our study rainfall was only weakly correlated with spawning of *Encrasicholina* at Munda (Tables 4, 5). Spawning appeared to be greater during periods of lower rainfall. Positive relationships between spawning and time since rain or less rain may be indirectly linked to phytoplankton production, which is determined by light or the depth of mixing (Wyatt 1980). Variations in wind strength and cloudiness will cause major variations in the onset and end of the phytoplankton production cycle (Blaxter and Hunter 1982). If rainfall at Munda is linked to the phytoplankton cycle, spawning during periods of low rainfall would be consistent with Cushing's (1967) hypothesis. Some previous studies in southeast Asia and Papua New Guinea (Tiews et al. 1971, Sitthichockpan 1972, Dalzell 1987b) have suggested that *Encrasicholina* spawned more intensively during the months of peak zooplankton production.

The variation in spawning frequency observed among the species in this study suggests that each responds differently to local conditions, reacting to those variables most appropriate to maximize reproductive success in the immediate environment (Bye 1984). No obvious differences were detected in baitfish spawning patterns between the exploited fishing grounds and the unexploited site. If baitfish numbers are higher at the unexploited site, this suggests, in turn, that differences in the observed spawning patterns were not density-dependent. Lack of clear proximate stimuli for spawning among the six species examined makes it difficult to predict the timing of major spawning events by these species.

However, protracted spawning and the baitfish population's adaptation to local conditions suggests that these species should be resilient to increased fishing mortality. Factors affecting larval survival and growth may be more important in determining recruitment to the fishery.

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# Biochemical Relationship Between Otolith and Somatic Growth in the Rainbow Trout *Oncorhynchus mykiss*: Consequence of Starvation, Resumed Feeding, and Diel Variations

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**Abstract.**–A biochemical examination of otolith growth–somatic growth relationship was conducted in rainbow trout *Oncorhynchus mykiss*. The rate of otolith growth was defined by calcium deposition on otoliths in an *in vitro* isolated preparation of otolith-containing sacculi. Somatic growth was estimated by RNA-DNA ratios in white trunk muscle. Rainbow trout weighing approximately 120 g were starved for 5 days and then fed commercial trout pellets once a day. They were sampled on days 1, 2, 3, and 5 after starvation, and on days 1, 2, 3, and 4 after feeding. In a separate experiment, fish were sampled at 6-hour intervals of 1000, 1600, 2200, and 0400 hours over a 24-hour period. Otolith and somatic growth showed a positive relationship, both decreasing from 2 days after starvation and recovering on day 4 after feeding. In otoliths, however, the starvation-induced decrease in calcium deposition was transiently restored on day 1 after feeding, followed by a decrease on day 2. The diel relationship between otolith and somatic growth was coupled, showing minimum levels at 2200 hours. These results suggest that otolith growth ordinarily reflects somatic growth rates on the daily basis.

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Teleost otoliths are calcium carbonate concretions which have increments consisting of a bipartite structure of light and dark rings. These structures are known to be formed on a daily basis (Pannella 1971). Since otolith and fish size are highly correlated for a variety of marine and freshwater species (Campana and Neilson 1985), it is possible to estimate growth-rate histories of individual fish by measuring the width of otolith increments. Volk et al. (1984) averaged otolith increment widths over each week and found a linear regression of mean increment width with somatic growth rate in chum salmon *Oncorhynchus keta* under controlled feeding. Nishimura and Yamada (1988) successfully back-calculated the growth rate of walleye pollock *Theragra chalcogramma* by using mean otolith width measured every 10 increments. However, it remains to be shown whether the rate of otolith growth reflects somatic growth rates in terms of daily or subdaily trends.

Recently several workers (Secor and Dean 1989, Reznick et al. 1989, Wright et al. 1990) reported an uncoupling of the relationship between otolith and somatic growth in fish populations experiencing slow and fast somatic growth. Similar uncoupling was exaggeratedly induced in hypophysectomized goldfish *Carassius auratus*, in which somatic growth in length was completely inhibited but otolith continued to grow at a reduced rate (Mugiya 1990).

Since the otolith (sagitta) occurs within the sacculus which is anatomically closed in rainbow trout *Oncorhynchus mykiss*, it is feasible to take out the otolith-containing sacculus without any leakage of the endolymph (Mugiya 1984). An *in vitro* preparation of the isolated sacculi was used for indicating the current growth rate of otoliths, which reflected the *in vivo* physiological state at the time when the fish were sampled (Mugiya 1984, 1987). Somatic growth is a balance between catabolic and anabolic components in protein metabolism (Miglavs and Jobling 1989). Since accretive growth should be directly associated with protein synthetic capacity, RNA-DNA ratios in muscle are widely used as an indicator of the short-term or current somatic growth rate (Bulow 1987).

The aim of the present study is to clarify the biochemical relationship between otolith and somatic growth on a daily basis, using starved and then fed rainbow trout. The otolith growth–fish growth relationship was also examined at 6-hour intervals

over a 24-hour period. Otolith and somatic growth were defined by the rate of *in vitro* calcium deposition on otoliths and RNA-DNA ratios in white trunk muscle, respectively. Serum calcium concentrations were examined for diel variations based on previous work on the relationship between serum calcium and otolith growth (Mugiya 1984).

## Materials and methods

We performed two experiments with food and diel effects on somatic and otolith growth. Immature rainbow trout *Oncorhynchus mykiss* weighing 100–130 g were obtained from a trout farm and acclimated to experimental conditions for at least 4 weeks before use. Throughout the acclimation and experimental periods, they were maintained in a pair of outside concrete ponds ($3.8\,m^2 \times 0.7\,m$ in depth) which were supplied with running water at $14 \pm 0.5°C$, and fed commercial trout pellets once a day at around 1500 hours, unless otherwise stated. The ration fed was about 1.5% of body weight.

### Starvation and refeeding

This experiment was carried out in October 1988. Dusk occurred at 1700 hours and dawn at 0545 hours. Sixty fish were randomly divided into two groups (30 fish per group), and separately assigned to one compartment of the paired ponds. One group was starved for 5 days and then fed. During these periods, they were sampled on days 1 (43 hours from last feeding), 2, 3, and 5 after starvation, and on days 1 (19 hours from the first refeeding), 2, 3, and 4 after refeeding. The other group was fed throughout the period and sampled as the control on the same time schedule, except on the third day of starvation and on the second day of refeeding when only the experimental group was sampled. Sampling was conducted alternately between experimental and control groups at 0945–1045 hours every day. At each sampling, 4–6 fish were gently netted one at a time, and immediately bled by cutting the tail of the fish. After bleeding, a pair of sacculi containing otoliths were isolated, placed in an incubation medium, and then the next fish was netted. The remaining part of the body was stored at −40°C and analyzed within 5 days for RNA-DNA ratios. Data from the control group were pooled for statistical analyses, as little difference was found among the sampling days.

### Diel variation

This experiment was carried out in December 1988. Dusk occurred in 1600 hours and dawn at 0700 hours. To examine the diel relationship between otolith and somatic growth, 25 fish were stocked in each compartment of the paired ponds, and 7 fish each were randomly sampled at 6-hour intervals of 1000, 1600, 2200, and 0400 hours over a 24-hour period. Sampling was conducted alternately from one compartment at 1000 and 2200 hours, and from the other compartment at 1600 and 0400 hours. This sampling regime is recommended for minimizing handling effects. After fish were netted one at a time, blood was immediately collected from the caudal vessels by cutting the tail of the fish and draining it into test tubes. After centrifugation, the separated sera were stored at −40°C for 6–24 hours and analyzed for total calcium concentrations by flame photometry using an atomic absorption spectrophotometer (Hitachi #518). After the blood collection, sacculi were isolated for incubation, and the remaining part of the body was stored for RNA and DNA analyses. In this experiment, the fish were starved throughout the sampling day.

### Otolith incubation

Otolith-containing sacculi were isolated according to a previously described technique (Mugiya 1987). Isolated sacculi were incubated in 50 mL of a Ringer solution (Mugiya 1986) containing $^{45}CA$ (New England Nuclear) at a concentration of $1 \times 10^4$ Bq/mL. Incubation was carried out with oxygenation at 14°C for 2 hours.

After incubation, sacculi were rinsed several times in $^{45}CA$-free Ringer solution and the otoliths were separated under a binocular microscope. The separated otoliths were lightly rinsed in water, placed in each counting vial, dried overnight at 80°C, and then weighed. They were solubilized in a mixture of 0.2 mL perchloric acid and 0.2 mL hydrogen peroxide (Mugiya 1987), and added to Scintisol EX-H (Wako Chem.) for radioactive counting (liquid scintillation spectrometer, Aloka LSC-673). The rate of otolith growth was evaluated in terms of micrograms of calcium deposited per unit otolith weight.

### RNA and DNA determinations

RNA-DNA ratios were estimated in the white muscle collected from an area of the dorsoanterior trunk, using a modification of the Schmidt and Thannhauser method (Buckley and Bulow 1987). Briefly, white muscle (1.00 g) was homogenized with cold distilled water and adjusted to 10.0 mL. A 1.4-mL aliquot of the homogenate was used for the estimation of nucleic acids. RNA and DNA were purified with 0.6N cold $HClO_4$, and then extracted with 0.3N KOH and 0.6N hot $HClO_4$, respectively. Both acids were quantified from the absorbance of the extracts at 260 nm. RNA and DNA

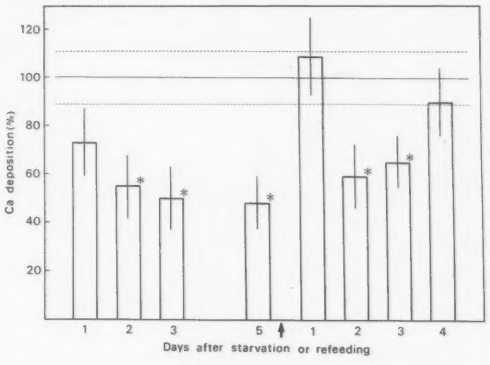


**Figure 1**

Percentage effects of starvation and refeeding on *in vitro* calcium deposition on otoliths in *Oncorhynchus mykiss*. Control values are pooled and the mean level (horizontal bar) is shown with SE of 48 otoliths. Vertical bars represent mean ± SE of 8–10 otoliths. Arrow indicates time when fish were refed. $^{*}P<0.05$.

**Table 1**

Effects of starvation and refeeding on muscle RNA and DNA concentrations (mg/g) in rainbow trout *Oncorhynchus mykiss*.

| | RNA | DNA |
|---|---|---|
| Control | 1.51 ± 0.03 | 0.61 ± 0.02 |
| Starvation (days) | | |
| 1 | 1.50 ± 0.06 | 0.56 ± 0.02 |
| 2 | 1.21 ± 0.08* | 0.58 ± 0.01 |
| 3 | 0.90 ± 0.04** | 0.65 ± 0.02 |
| 5 | 0.89 ± 0.04** | 0.68 ± 0.04 |
| Refeeding (days) | | |
| 1 | 0.88 ± 0.07** | 0.65 ± 0.06 |
| 2 | 0.97 ± 0.06** | 0.61 ± 0.02 |
| 3 | 1.07 ± 0.02** | 0.66 ± 0.01 |
| 4 | 1.57 ± 0.04 | 0.63 ± 0.02 |

Values are mean ± SE of 26 and 4–6 fish for control and experimental groups, respectively.
$^{*}P<0.05$; $^{**}P<0.01$.

standard solutions were prepared using RNA from yeast and DNA from salmon sperm (Wako Chem.).

### Statistics

Student's $t$-test for unpaired observations was applied to assess statistical significance of differences between mean values. Significance was accepted at $P<0.05$.

## Results

### Starvation and refeeding

The rate of *in vitro* calcium deposition on otoliths ranged from 0.06 to 0.08 μg/mg·hour in the control group. These data are pooled and presented as the mean level with standard errors (Fig. 1). Effects of starvation and refeeding on the rate are expressed as a percentage against the control level. Starvation induced an inhibitory effect ($P<0.05$) on the rate of calcium deposition on otoliths by day 2, decreasing to approximately half of the control. This level remained almost unchanged until day 5, the last day of starvation. On refeeding, the starvation-induced decrease recovered to the control level as early as day 1. However, this recovery was transient, followed by a significantly ($P<0.05$) reduced calcium deposition on day 2. This reduced calcium deposition recovered to the control level on day 4 after refeeding (Fig. 1).

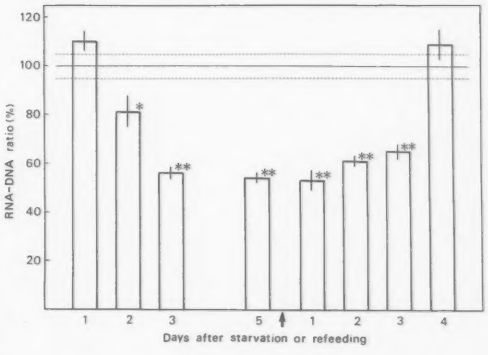


**Figure 2**

Percentage effects of starvation and refeeding on RNA-DNA ratios in white trunk muscle in *Oncorhynchus mykiss*. Control values are pooled and the mean level (horizontal bar) is shown with SE of 26 fish. Vertical bars represent mean ± SE of 4 or 6 fish. Arrow indicates time when fish were refed. $^{*}P<0.05$; $^{**}P<0.01$.

Muscle RNA and DNA concentrations and their ratios are presented in Table 1 and Figure 2, respectively. Starvation and refeeding affected RNA concentrations, but DNA concentrations remained constant during the experiment (Table 1). Therefore, changes in RNA-DNA ratios are primarily attributable to changes in RNA concentrations.

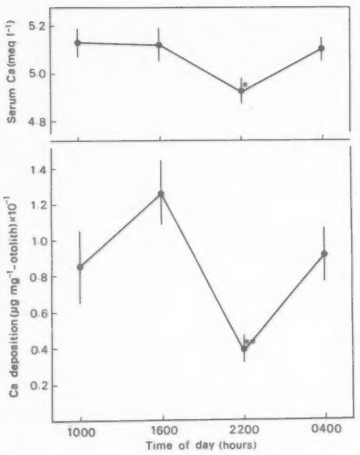


**Figure 3**

Diel variations in serum calcium concentrations (upper graph) and *in vitro* calcium deposition on otoliths (lower graph) in *Oncorhynchus mykiss*. Each plotted value represents mean ± SE of 7 fish for serum calcium and of 12–14 otoliths. *$P<0.05$ for 1600 hours; **$P<0.001$ for 1600 hours.

**Table 2**

Diel variations in muscle RNA and DNA concentrations (mg/g) in rainbow trout *Oncorhynchus mykiss*.

| Time of day (h) | RNA | DNA |
|---|---|---|
| 1000 | 1.26 ± 0.08 | 0.66 ± 0.04 |
| 1600 | 1.30 ± 0.08 | 0.72 ± 0.02 |
| 2200 | 0.66 ± 0.04* | 0.76 ± 0.06 |
| 0400 | 0.80 ± 0.04 | 0.68 ± 0.04 |

Values are mean ± SE of 7 fish.
*$P<0.01$ for 1600 hours.

RNA-DNA ratios ranged from 1.91 to 2.73, with a mean value of 2.44 in the control group. One day's starvation had no effect on the ratio (Fig. 2). The first significant ($P<0.05$) effect occurred on day 2 after starvation, followed by further decrease to approximately half of the control on day 3. This reduced level apparently remained essentially unchanged through day 5. In contrast to the response observed for otoliths, refeeding had no effect on the recovery in RNA-DNA ratios the next day (Fig. 2). Ratios increased gradually with feeding and recovered to the control level on day 4 after refeeding.

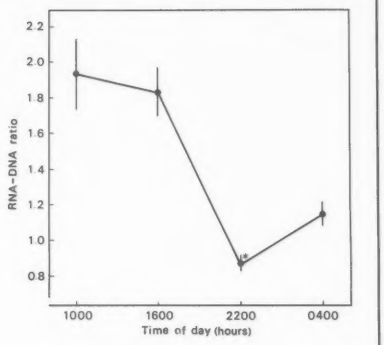


**Figure 4**

Diel variations in RNA-DNA ratios in white trunk muscle in *Oncorhynchus mykiss*. Each plotted value represents mean ± SE of 7 fish. *$P<0.001$ for 1600 hours.

## Diel variation

Serum calcium concentrations varied dielly by approximately 4%, and this variation was statistically significant at $P = 0.05$ (Fig. 3). Calcium concentrations were high during the daytime, but a nadir occurred at 2200 hours.

The profile of diel variations in calcium deposition on otoliths was essentially the same as that of serum calcium concentrations (Fig. 3). The high rate of calcium deposition at 1600 hours rapidly decreased by 70% ($P<0.001$) to a nadir at 2200 hours, followed by an increase toward 0400 hours.

Diel variations in muscle RNA and DNA concentrations and their ratios are presented in Table 2 and Figure 4, respectively. Diel variations were significant in RNA concentrations and RNA-DNA ratios. The profile of variations in the ratios was similar to that of calcium deposition on otoliths: high ratios during the daytime were followed by a steep decrease between 1600 and 2200 hours. The lowest ratio occurred at 2200 hours, and this ratio was highly significant ($P<0.001$) compared with the ratio at 1600 hours. Differences between 1000 and 1600 hours were not statistically significant in either otolith or muscle, showing that the criterion of similar growth profiles was fulfilled.

A comparison of variations in calcium deposition on otoliths and RNA-DNA ratios in muscle showed positive relationships through several days after starvation and during the diel experiment. However, uncoupling was found in the recovery processes with refeeding: calcium deposition on otoliths transiently recovered on day 1 after refeeding, while RNA-DNA ratios did not (compare Figures 1 and 2).

## Discussion

RNA-DNA ratios in muscle have been widely accepted as an index of current somatic growth rates in various species of marine and freshwater fish (Bulow 1987). These ratios are affected by various factors such as season (Bulow et al. 1981), ration size (Bulow 1970, Buckley 1979, Wilder and Stanley 1983, Jürss et al. 1986), temperature, salinity (Jürss et al. 1987), and lunar cycles (Farbridge and Leatherland 1987). Various toxicants also reduce the ratios (Barron and Adelman 1984). The present study presents an additional finding with regard to variations of RNA-DNA ratios: the ratios had distinct diel variations, showing higher values during daytime than nighttime. It is desirable to confirm such a profile of variations by further examinations at shorter and longer time-intervals.

Endocrinologically, RNA-DNA ratios are under the control of growth-regulating hormones. Hypophysectomy reduced the ratios, and replacement therapy with beef growth hormone restored the ratios to a normal level in bullheads *Ictalurus melas* (Kayes 1979). Circadian periodicities in the surge of growth-regulating hormones are well documented in higher vertebrates (Kato et al. 1982). Although few comparable references are available in fish, cyclic variations in growth hormone have been reported in plasma and pituitary levels in salmonids (Leatherland et al. 1974, Leatherland and Nuti 1982, Bates et al. 1989). Therefore, the cyclic surge of this hormone in combination with other hormones is probably a cause for diel variations in RNA-DNA ratios in the present fish.

Effects of starvation or restricted food on RNA-DNA ratios have been repeatedly reported. A 4-week starvation induced an approximately 40% decrease in the ratios in rainbow trout *Oncorhynchus mykiss* (Jürss et al. 1986). Brook trout *Salvelinus fontinalis* also had the ratio reduced by 44% after 22 days of restricted feeding (Wilder and Stanley 1983). Bulow (1970) showed that RNA-DNA ratios directly reflected different somatic growth rates induced by nutritional manipulation. However, it is not clear how fast food deprivation affects this ratio. Although the time course of the effect will depend on various factors such as temperature, fish sizes, sexual status, etc., the present study revealed that the first effect of starvation on RNA-DNA ratios in muscle appeared on day 2 (67 hours from last feeding) in adult rainbow trout *Oncorhynchus mykiss*. This inhibitory effect was exaggerated with time, but the ratios never decreased below half the control level even on day 15 after starvation (data are not presented here). This level (55% of the control) is similar to trout values in the literature mentioned above, and therefore it appears to be a basal level in RNA-DNA ratios in white muscle of rainbow trout.

Starvation-induced decrease in RNA-DNA ratios recovered with the resumption of daily feeding at a level of 1.5% of body weight. The recovery processes were rather steady, taking 4 days in the present study. Bulow (1970) showed a more rapid recovery in golden shiners *Notemigonus crysoleucas*: 2 days feeding at 6% body weight seemed to be enough for the recovery of a starvation-induced decrease in ratios to the normal level. This disparity may be explained by the amount of food used and/or species difference. Lied et al. (1983) reported that a starvation-induced decrease in RNA-DNA ratios recovered to the normal level within 8 hours after refeeding *ad libitum* in cod *Gadus morhua*. However, it is uncertain whether this recovery was due to the result of food assimilation or to diel variations in the ratios, because control values were not available at each determination time in the study.

Recently Miglavs and Jobling (1989) reported that a growth spurt (compensatory growth) transiently occurred following realimentation after a period of food restriction in juvenile Arctic char *Salvelinus alpinus*. Nevertheless, no corresponding increase occurred in tissue RNA-DNA ratios. This led them to present a limit to using the ratios as a growth index. However, since their somatic growth rate was calculated from a cumulated increase in body weight for 28 days, it is uncertain whether or not the rate remained high on the last day, when the RNA-DNA ratios were determined.

When somatic and otolith growth rates were biochemically compared at 6-hour intervals over a 24-hour period, or after food deprivation, they were coupled at a qualitative level. In spite of these positive relationships, evidence of an allometric relationship between otolith and somatic growth has been accumulated, especially under suboptimal conditions. For example, Mosegaard et al. (1988) examined the effect of temperature, fish size, and somatic growth rate on otolith growth rate in Arctic char *Salvelinus alpinus* and found an uncoupling between somatic and otolith growth rates at hyperoptimal temperatures. Based on these results, they suggested that metabolic activity, not necessarily somatic growth rate, governs otolith growth rate. Somatic growth rate results mainly from the balance between protein synthesis and degradation, and hyperoptimal temperatures would accelerate both components, especially degradation, resulting in no somatic growth (Houlihan et al. 1988). However, since somatic growth is comparable with components from metabolic rates within the range of optimal temperatures (Webb 1978), the muscle RNA-DNA ratio, an index for protein synthesis, will be a reflection of metabolic components at an appropriate temperature. Therefore, it appears reasonable to use this ratio for examining the relationship between somatic and otolith growth rates, even if otolith growth is a function of metabolic rate.

In the present study, the transient recovery of otolith growth occurred on the first day following refeeding. Although the definite reason for this remains unexplained, an accelerated recovery process after growth suppression is well known as "repletion" in mammalian skeletal tissue formation (Linkhart et al. 1988). Mechanisms for repletion would differ depending on tissues. Since the otolith is an acellular product secreted by otolith-forming cells (Saitoh and Yamada 1989), a possible explanation for otolith repletion is as follows: Starvation may interrupt the releasing activity partly due to the reduced processing of the secretory product. This would inversely result in some accumulation of otolith precursor materials in the cells (Anderson and Capen 1976). Refeeding stimulates release of the accumulated precursors through some factors (e.g., calcium-calmodulin interaction; Mugiya 1986) regulating the secretory activity. A steady-state recovery in synthesis and processing of the secretory product is probably a time-consuming process, running parallel to the recovery of RNA-DNA ratios in muscle. These possibilities await further examination.

In the present study, we have demonstrated corresponding variations in otolith calcification and RNA-DNA ratios in muscle, but a causal relationship between specific growth rate and otolith calcification remains to be studied.

## Acknowledgments

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# Western Atlantic Tonguefishes of the *Symphurus plagusia* Complex (Cynoglossidae: Pleuronectiformes), with Descriptions of Two New Species*

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**Abstract.** – Western Atlantic tonguefishes of the *Symphurus plagusia* (Schneider, in Bloch and Schneider 1801) complex are distinguished from other Atlantic *Symphurus* species by the possession of 12 caudal fin rays, a 1-4-3 pattern of interdigitation of dorsal-fin pterygiophores and neural spines, absence of a pupillary operculum, reduced or absent dentition on ocular-side jaws, and an unpigmented peritoneum. Considerable taxonomic uncertainty has been associated with nominal species of this complex, but the most common practice has been to recognize one widespread species (*S. plagusia*) with two subspecies ranging from the Caribbean southward to Uruguay, and a second species, *S. civitatium* Ginsburg 1951, occurring in inshore areas along the southeastern and Gulf of Mexico coasts of the United States and northern Mexico. The validity of *S. civitatium* is confirmed in this study. Examination of tonguefishes from the Caribbean and southward indicates that specimens previously identified as *S. plagusia* do not comprise one species with two allopatric subspecies, but rather four largely sympatric, albeit not necessarily syntopic, species. *Symphurus plagusia*, the first described species in this complex, occurs in inshore habitats ranging from the Caribbean to Rio de Janeiro. *Symphurus tessellatus* (Quoy and Gaimard 1824), removed from the synonymy of *S. plagusia*, occurs in nearshore, estuarine, and neritic waters throughout the Caribbean southwards to Uruguay. Two new species, *S. oculellus* occurring in neritic waters off northern South America (Guyana to northern Brazil), and *S. caribbeanus* (nearshore habitats throughout the Caribbean), are described and figured. A key to the western Atlantic species of this complex is provided.

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Shallow-water symphurine tonguefishes possessing 12 caudal fin rays, a 1-4-3 pattern of interdigitation of dorsal pterygiophores and neural spines, with reduced or absent dentition on ocular-side jaws, an unpigmented peritoneum, and lacking a pupillary operculum comprise the *Symphurus plagusia* (Schneider, in Bloch and Schneider 1801) complex.** Five western Atlantic and several eastern Pacific species of tonguefishes are recognized in this complex. Throughout the western Atlantic, from North Carolina, U.S.A., to Uruguay (Ginsburg 1951, Menezes and Benvegnú 1976, Munroe 1987), these commonly collected tonguefishes are abundant locally in estuarine and nearshore habitats as well as on sandy or muddy substrates on the inner continental shelf (Meek and Hildebrand 1928, Ginsburg 1951, Lowe-McConnell 1962, Caldwell 1966, Cervigon 1966, Carvalho et al. 1968, Palacio 1974, Menezes and Benvegnú 1976, Lema and Oliveria 1977, Lema et al. 1980, Munroe 1987).

Nomenclatural uncertainty and questions regarding taxonomic validity have been associated with these western Atlantic tonguefishes since the first description of a species from Jamaica by Browne (1756). Much of the confusion centers on species collected in shallow waters of the Caribbean and coastal seas of Central America and much of South America. At least ten combinations of names have been used for these tropical western Atlantic, shallow-water tonguefishes.

Historically (Kaup 1858, Jordan and Evermann 1898, Chabanaud 1949), Atlantic members of this species complex were long regarded as comprising populations of a single widespread, polytypic species, *Symphurus plagusia*. This nomenclatural arrangement began with Kaup (1858) and has continued to the present (Jordan and Goss 1889, Jordan and Evermann 1898, Ginsburg 1951, Menezes and Benvegnú 1976, Rosa 1980, Lucena and Lucena 1982). Ginsburg considered the tropical western Atlantic members of this complex to represent two allopatric subspecies, and his newly-described *S. civitatium* with its disjunct northern distribution, perhaps representing a third subspecies of one wide-ranging polytypic species. However, the most recent review of *Symphurus* of southern South America (Menezes and Benvegnú 1976) questioned recog-

* Contribution no. 1659 of the Virginia Institute of Marine Science, College of William and Mary.

** There is another western Atlantic tonguefish, *S. plagiusa* (Linnaeus), completely allopatric from *S. plagusia*, which unfortunately has a nearly identical spelling for its specific epithet. It is emphasized that these are completely different and distinctive species that should not be confused because of similarities in their names.

nition of only one species in the tropical western Atlantic region.

My examination of approximately 1000 specimens of *Symphurus* possessing 12 caudal fin rays and a 1-4-3 interdigitation pattern, collected in inshore waters from North Carolina, throughout the Gulf of Mexico and Caribbean, to Uruguay, reveals that previous studies failed to recognize the presence of multiple sympatric species among their material. Neither the hypothesis of multiple populations within a single polytypic species, envisioned especially by Jordan and co-workers, nor Ginsburg's hypothesis of one widespread polytypic species comprised of allopatric subspecies, adequately explain the divergent morphological variation observed in the specimens and the sympatric (sometimes syntopic) occurrences of specimens with different morphological attributes. Instead, the present study recognizes not one, but rather five, western Atlantic members of the *S. plagusia* complex, which are somewhat phenetically similar species that differ in morphology and pigmentation. Four of these species have largely sympatric, but not necessarily syntopic, distributions. The fifth species, *S. civitatium* Ginsburg 1951, is completely allopatric to the others, occurring along the southeastern and Gulf coasts of the United States and northern Mexico.

Three species in this assemblage, *S. plagusia*, *S. tessellatus* (Quoy and Gaimard 1824), and *S. civitatium*, were described previously. Two additional species are described herein. Available taxonomic and ecological information is summarized, differential diagnoses are provided for each species, and a key to identification of the five species is included.

## Materials and methods

Methods for counts and measurements and general terminology follow Munroe and Mahadeva (1989) and Munroe (1990). Meristic data, exclusive of scale counts, were taken from radiographs. ID pattern refers to the pattern of interdigitation of dorsal pterygiophores and neural spines. In species accounts, total ranges for meristic features are presented first, followed by modal counts when data were sufficient.

Measurements less than 150 mm were taken to the nearest 0.1 mm with dial calipers or ocular micrometer. Measurements over 150 mm were taken to the nearest mm with a steel ruler. Measurements are expressed either as thousandths of standard length (SL) or thousandths of head length (HL).

### Morphometric abbreviations

**ABL** anal fin length
**BD** body depth
**CD** chin depth
**CFL** caudal fin length
**DBL** dorsal fin length
**ED** eye diameter
**HL** head length
**HW** head width
**LHL** lower head lobe width
**OPUL** width of upper opercular lobe
**OPLL** width of lower opercular lobe
**PA** pelvic to anal fin length
**PAL** preanal length
**PDL** predorsal length
**PL** pelvic fin length
**POL** postorbital length
**SNL** snout length
**UHL** upper head lobe width
**UJL** upper jaw length

All descriptions of pigmentation are based on fishes fixed in formalin and stored in ethyl or isopropyl alcohol.

Maturity was estimated by macroscopic examination of stages of developing ova and extent of posterior elongation of the ovaries (ovaries of mature females are sometimes conspicuous through the body wall in transmitted light; in immature females and large females, ovaries are best observed by dissection). Since no obvious differences in male testicular size were apparent, estimates of maturity were based entirely on females. Immature females were those with nonelongate or only partially elongate ovaries. Mature females had fully elongate ovaries. Gravid females were those individuals with enlarged ovaries filled with large, macroscopically visible ova.

When available, depth-of-capture information (converted to the nearest meter) was recorded and summarized for specimens listed in the "Material examined" sections in each species account. If depth of capture included a range of depths over which the nets were towed, a mean depth for that particular trawl was calculated.

Synonomies are selective for *S. plagusia* and *S. tessellatus* because of the numerous locality citations; synonomies are presumed to be complete for the other species. Because of their common occurrence, *S. plagusia* and *S. tessellatus* are listed in numerous studies, beginning with the oldest literature dealing with shallow-water marine fish faunas of the Caribbean and temperate regions of eastern South America. Since little descriptive or ecological information was provided in most original accounts of these tonguefishes, it is often impossible, when reviewing the literature, to determine accurately the species studied. For example, in studies of tonguefishes occurring in the Caribbean and along the coasts of Central and northern

South America, the possibility exists of any combination of four species being considered in the accounts. Since many of these earliest studies of Caribbean fishes considered only shore-zone fishes, much of this literature is discussed under the account of *S. plagusia*, one of the more widely distributed shallow-water species, and the one first named in the complex. Most references from extreme southern South America pertaining to shallow-water tonguefishes possessing 12 caudal fin rays refer to *S. tessellatus* and are included in the synonymy of that species. Synonymies for the remaining species include only those studies from which I examined specimens.

### Abbreviations of institutions

Institutions providing study material, or in which type material is deposited are:

**ALA** Museum of Natural History, University of Alabama, University
**ANSP** Academy of Natural Sciences, Philadelphia
**BMNH** British Museum of Natural History, London
**CAS-SU** California Academy of Sciences, San Francisco
**FMNH** Field Museum of Natural History, Chicago
**GCRL** Gulf Coast Research Laboratory, Ocean Springs
**IMS** Marine Sciences Institute, University of Texas at Austin, Port Aransas
**LACM** Natural History Museum of Los Angeles County, Los Angeles
**MCP** Museu de Ciencias, Pontificia Universidade Catolica do Rio Grande do Sul, Porto Alegre
**MCZ** Museum of Comparative Zoology, Harvard University, Cambridge
**MHNN** Musee d'Histoire Naturelle de Neuchâtel, Neuchâtel
**MNHN** Museum National d'Histoire Naturelle, Paris
**TCWC** Texas Cooperative Wildlife Collection, Texas A&M University, College Station
**TU** Department of Zoology, Tulane University, New Orleans
**UF** Florida State Museum, University of Florida, Gainesville
**UFPB** Departamento de Sistematica e Ecologia, Universidade Federal da Paraiba, Joao Pessoa
**UMML** Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami
**UMMZ** Museum of Zoology, University of Michigan, Ann Arbor
**UPRM** University of Puerto Rico at Mayaguez
**USA** University of South Alabama, Mobile
**USNM** National Museum of Natural History, Smithsonian Institution, Washington, DC
**ZMA** Zoologisch Museum, Universiteit van Amsterdam

## Artificial key to Western Atlantic members of the *Symphurus plagusia* complex

**1a** Large black spot on outer margin of ocular-side opercle; dorsal fin rays 91–107; anal fin rays 77–89; total vertebrae 50–55 ..... 2

**1b** No obvious black spot on ocular-side opercle; dorsal fin rays 86–97; anal fin rays 70–81; total vertebrae 46–51 ..... 3

**2a** 4–8 small ctenoid scales on blind side of posterior rays of dorsal and anal fins; ocular-side lower jaw without fleshy ridge on posterior portion; jaws reaching only to rear margin of pupil or rear margin of eye; crossbands wide, usually nine or less; posterior third of dorsal and anal fins without alternating series of pigment blotches and unpigmented areas, usually becoming increasingly darker posteriorly (black in mature males); dorsal fin rays 91–102; anal fin rays 77–86; total vertebrae usually 50–53. (Caribbean Sea to Uruguay) ..... ***S. tessellatus* (Quoy and Gaimard)**

**2b** No ctenoid scales on blind side of posterior rays of dorsal and anal fins; ocular-side lower jaw usually with pronounced fleshy ridge on posterior portion; jaws reaching rear margin of lower eye or extending slightly posterior to rear margin of lower eye; crossbands narrow, usually 10–14; dorsal and anal fins with alternating series of blotches and unpigmented areas, usually not becoming darker posteriorly; dorsal fin rays 99–106; anal fin rays 81–88; total vertebrae usually 53–54. (Guyana to northern Brazil) ..... ***S. oculellus* new species**

**3a** Dorsal and anal fins with an alternating series of dark blotches and unpigmented areas; ocular-side lower jaw without fleshy ridge on posterior portion; snout pointed; distance between upper eye and dorsal fin base usually slightly smaller than twice eye diameter; body with 9–15, narrow, dark crossbands; eye usually 9.0–10.0% of HL. (Caribbean Sea) ..... ***S. caribbeanus* new species**

**3b** Dorsal and anal fins usually uniformly pigmented, without obvious pigmented blotches; ocular-side lower jaw usually with pronounced fleshy ridge on posterior portion; snout squarish; distance from upper eye to dorsal fin base usually larger than twice eye diameter; body uniformly colored or with 4–9 faint crossbands; eye 6.4–11.0% HL, usually only 6.4–9.4% HL ..... **4**

**4a** Eye usually only 6.4–9.5% HL; total vertebrae 49–51; dorsal fin rays 91–97; anal fin rays 75–81; longitudinal scales 79–89. (Caribbean Sea to southern Brazil) ..... ***S. plagusia* (Schneider, in Bloch and Schneider)**

**4b** Eye 7.0–11.0% HL, usually 8.0–10.0% HL; total vertebrae usually 47–49; dorsal fin rays 86–93; anal fin rays 70–78; longitudinal scales 66–83. (Gulf of Mexico and southeastern United States) ..... ***S. civitatium* Ginsburg**

**Table 1**
Frequency distributions of predominant patterns of interdigitation of dorsal pterygiophores and neural spines (ID pattern) observed in five western Atlantic species of the *Symphurus plagusia* complex.

| | ID pattern | | | | | | |
|---|---|---|---|---|---|---|---|
| Species | 1-3-3 | 1-3-4 | 1-4-2 | 1-4-3 | 1-4-4 | 1-5-2 | 1-5-3 |
| *civitatium* | 8 | 6 | 19 | 127 | — | 7 | 3 |
| *plagusia* | 4 | 1 | 2 | 32 | 1 | — | 1 |
| *tessellatus* | 10 | 16 | 11 | 177 | 12 | 3 | 14 |
| *oculellus* | 1 | 2 | 1 | 33 | — | — | 1 |
| *caribbeanus* | 8 | 3 | — | 69 | 2 | 2 | |

**Table 2**
Frequency distributions of the numbers of caudal fin rays for five western Atlantic species of the *Symphurus plagusia* complex.

| | Caudal fin ray count | | | |
|---|---|---|---|---|
| Species | 10 | 11 | 12 | 13 |
| *civitatium* | | 8 | 163 | |
| *plagusia* | | 2 | 39 | 1 |
| *tessellatus* | 4 | 11 | 216 | 2 |
| *oculellus* | | 4 | 49 | |
| *caribbeanus* | 1 | 2 | 80 | 1 |

**Table 3**
Frequency distributions of the numbers of dorsal fin rays for five western Atlantic species of the *Symphurus plagusia* complex.

| | Dorsal fin ray number | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | $\bar{x}$ |
| *civitatium* | 2 | 3 | 14 | 33 | 49 | 46 | 23 | 1 | | | | | | | | | | | | | | 90.1 |
| *plagusia* | | | | 1 | — | 4 | 11 | 12 | 4 | 4 | 5 | 1 | | | | | | | | | | 93.2 |
| *tessellatus* | | | | | | 2 | 2 | 6 | 16 | 40 | 30 | 53 | 36 | 28 | 19 | 9 | 1 | | | | | 96.9 |
| *oculellus* | | | | | | | | | | | | | | 4 | 14 | 17 | 9 | 5 | 2 | — | 1 | 101.2 |
| *caribbeanus* | | | | 1 | — | 1 | 13 | 29 | 25 | 10 | 5 | | | | | | | | | | | 93.5 |

**Table 4**
Frequency distributions of the numbers of anal fin rays for five western Atlantic species of the *Symphurus plagusia* complex.

| | Anal fin ray number | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | $\bar{x}$ |
| *civitatium* | 1 | 2 | 6 | 34 | 49 | 57 | 20 | 3 | 1 | | | | | | | | | | | | | 74.3 |
| *plagusia* | | | | 1 | — | 5 | 8 | 15 | 5 | 6 | 1 | 1 | | | | | | | | | | 77.0 |
| *tessellatus* | | | | | | | | 5 | 24 | 36 | 45 | 45 | 37 | 26 | 18 | 3 | 1 | | | | | 80.8 |
| *oculellus* | | | | | | | | | | | | 1 | 2 | 5 | 17 | 17 | 5 | 5 | 1 | 2 | | 84.8 |
| *caribbeanus* | | | | | 1 | 3 | 6 | 24 | 40 | 6 | 3 | | | | | | | | | | | 77.6 |

**Table 5**

Frequency distributions of the numbers of total vertebrae for five western Atlantic species of the *Symphurus plagusia* complex.

| | Vertebrae number | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | $\bar{x}$ |
| *civitatium* | 2 | 34 | 108 | 28 | 2 | | | | | | 48.0 |
| *plagusia* | | 1 | 4 | 20 | 12 | 5 | | | | | 49.4 |
| *tessellatus* | | | | 3 | 47 | 87 | 71 | 32 | 2 | | 51.4 |
| *oculellus* | | | | | | | 2 | 23 | 11 | 1 | 53.3 |
| *caribbeanus* | | | 1 | 43 | 33 | 4 | | | | | 49.5 |

**Table 6**

Frequency distributions of the numbers of longitudinal scale rows for five western Atlantic species of the *Symphurus plagusia* complex.

| | Scale rows | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | $\bar{x}$ |
| *civitatium* | 1 | — | — | — | 2 | — | — | 1 | 4 | 8 | 11 | 5 | 14 | 8 | 7 | 3 | 3 | 1 | | | | | | | 77.2 |
| *plagusia* | | | | | | | | | | | | | | 1 | 3 | 2 | 3 | 2 | 2 | 1 | 3 | — | — | 2 | 83.3 |
| *caribbeanus* | | | | | | | | | | | | | 3 | — | 4 | 11 | 4 | 3 | 6 | 2 | 2 | 1 | 1 | 3 | 82.8 |

| | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | $\bar{x}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *tessellatus* | 2 | 2 | 8 | 10 | 10 | 11 | 21 | 31 | 21 | 21 | 14 | 5 | 4 | 2 | — | 1 | | 87.9 |
| *oculellus* | | | | 1 | 3 | 1 | 7 | 5 | 2 | 6 | 4 | 2 | — | 1 | — | — | 1 | 89.8 |

**Table 7**

Frequencies of the numbers of scale rows between the posterior margin of the eyes to the midpoint emargination of the opercle for five western Atlantic species of the *Symphurus plagusia* complex.

| | Scale rows | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | $\bar{x}$ |
| *civitatium* | 3 | 18 | 32 | 16 | 3 | | | | 18.0 |
| *plagusia* | | | 8 | 4 | 8 | 2 | 1 | | 19.3 |
| *tessellatus* | | | 1 | — | 8 | 9 | 4 | 1 | 20.8 |
| *oculellus* | | | | 3 | 8 | 1 | 1 | 2 | 20.4 |
| *caribbeanus* | | 1 | 1 | 9 | 16 | 8 | 3 | | 20.0 |

**Table 8**

Frequency distributions of the transverse scale count observed for five western Atlantic species of the *Symphurus plagusia* complex.

| | Scale count | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | $\bar{x}$ |
| *civitatium* | 2 | 1 | 2 | — | 2 | 5 | 4 | 6 | 2 | 11 | 5 | 6 | 6 | 1 | | | | | | | 33.9 |
| *plagusia* | | | | | | | | | | 1 | — | — | 2 | 3 | 7 | 3 | 3 | 1 | | | 40.0 |
| *tessellatus* | | | | | | | | | | | | | 1 | 2 | 4 | 5 | 3 | 1 | 3 | 2 | 41.5 |
| *oculellus* | | | | | | | | | | | 1 | 1 | 6 | 2 | 2 | 1 | 1 | | | | 38.7 |
| *caribbeanus* | | | | | | | | | | | 2 | 3 | 6 | 10 | 3 | 6 | 2 | 1 | 1 | | 39.4 |

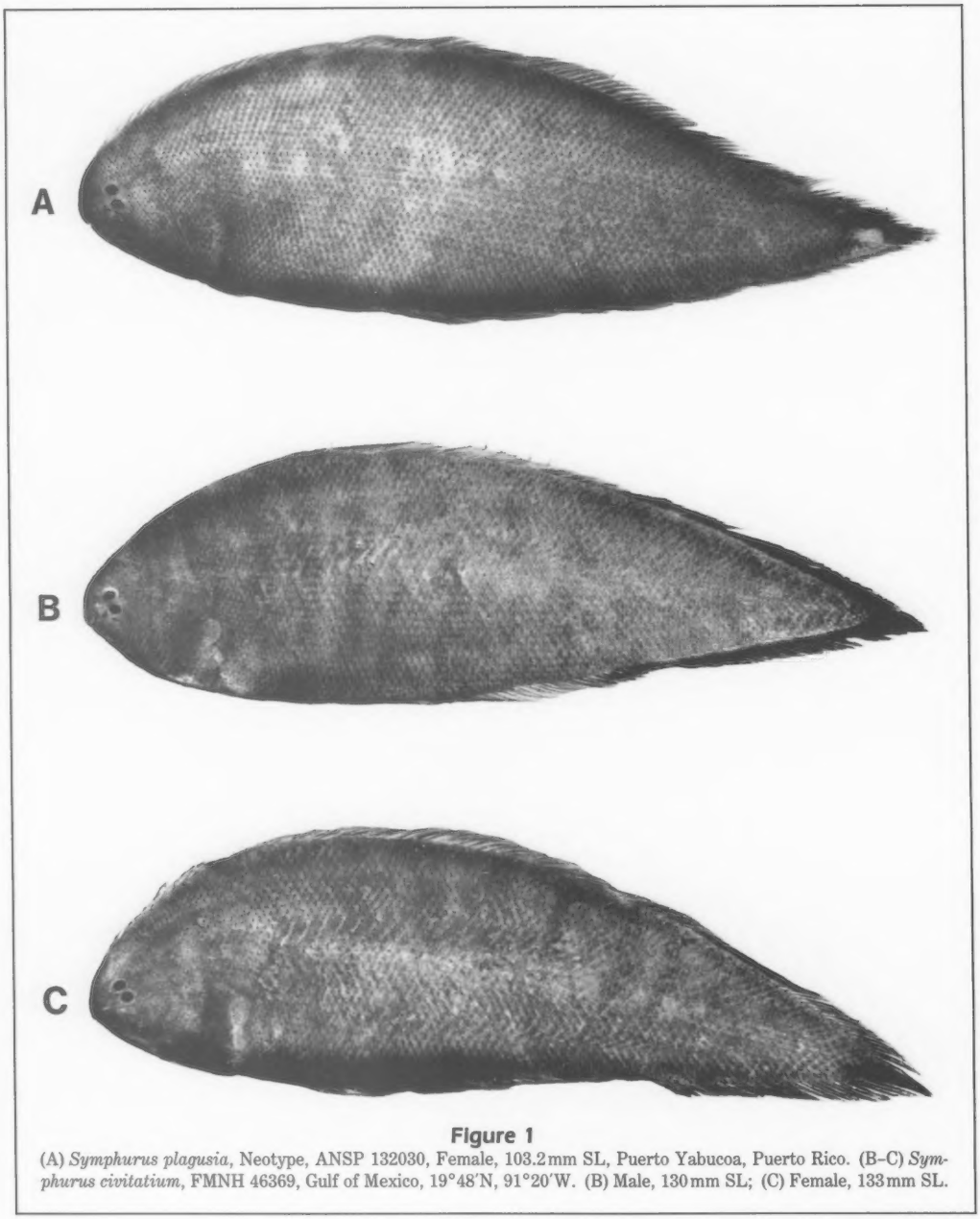



**Figure 1**

(A) *Symphurus plagusia*, Neotype, ANSP 132030, Female, 103.2 mm SL, Puerto Yabucoa, Puerto Rico. (B–C) *Symphurus civitatium*, FMNH 46369, Gulf of Mexico, 19°48′N, 91°20′W. (B) Male, 130 mm SL; (C) Female, 133 mm SL.

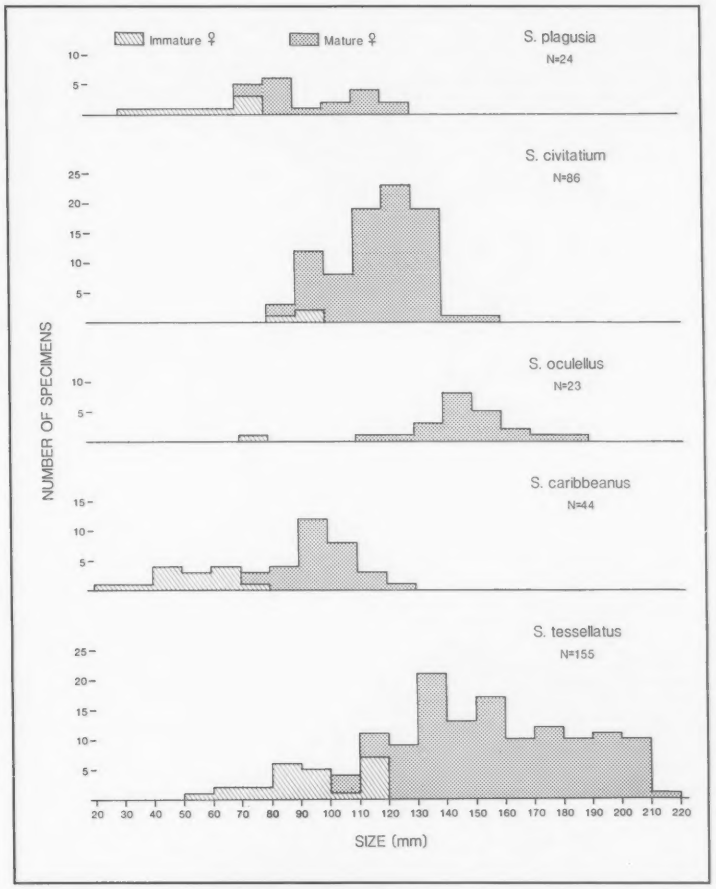



**Figure 2**
Frequency histogram of size distributions (standard length) and relative sizes at sexual maturity for females of five western Atlantic species of the *Symphurus plagusia* complex. Mature females were those with fully elongate ovaries. Immature females were those with non-elongate or only partially elongate ovaries.

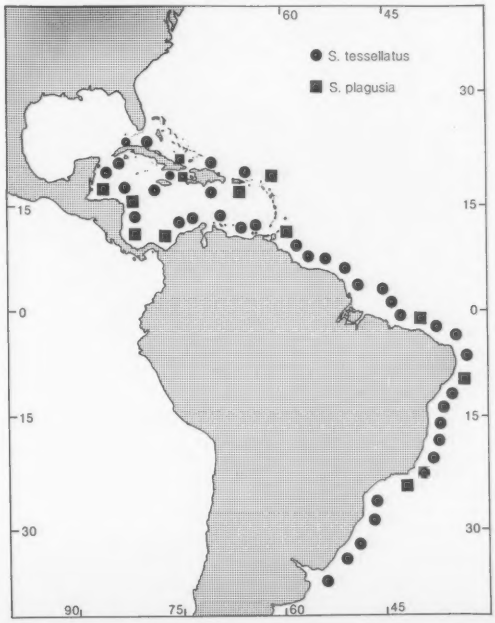



**Figure 3**
Geographic distributions of *Symphurus plagusia* and *S. tessellatus* based on material examined.

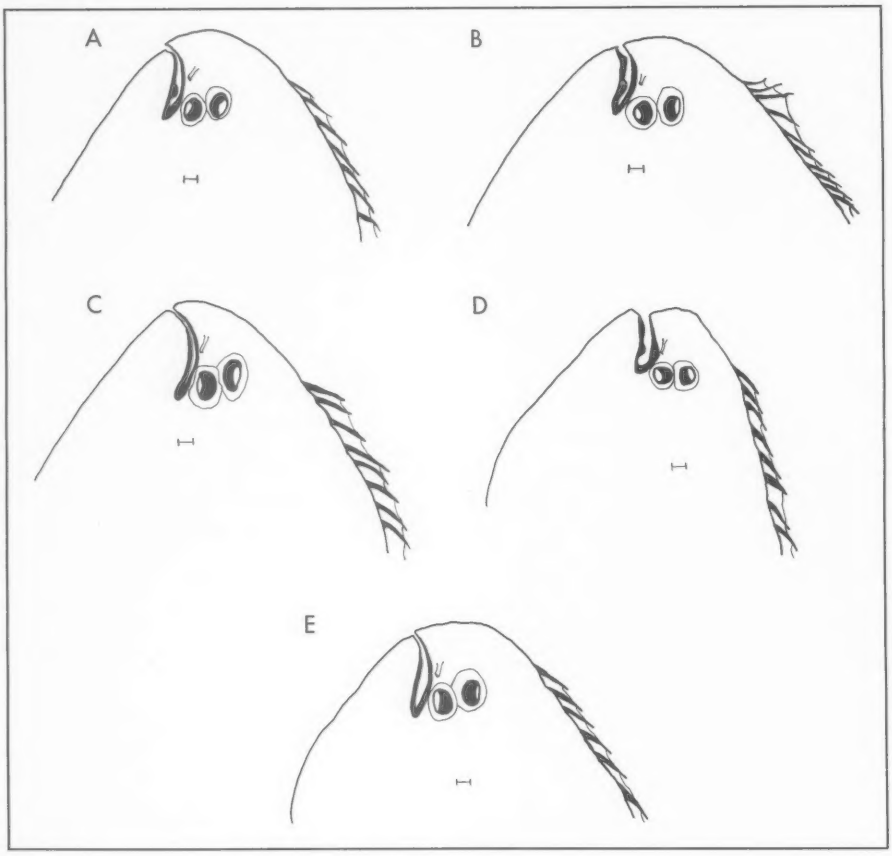



**Figure 4**
Schematic illustration of ocular-side lower jaws, head shapes, and relative positions of the dorsal fin origin for five western Atlantic tonguefishes of the *Symphurus plagusia* species complex. (A) *S. plagusia*, ANSP 132030. (B) *S. civitatium*, USNM 274485. (C) *S. tessellatus*, UPRM 2859. (D) *S. oculellus*, UMML 34334. (E) *S. caribbeanus*, USNM 313487. Bar = 1 mm.

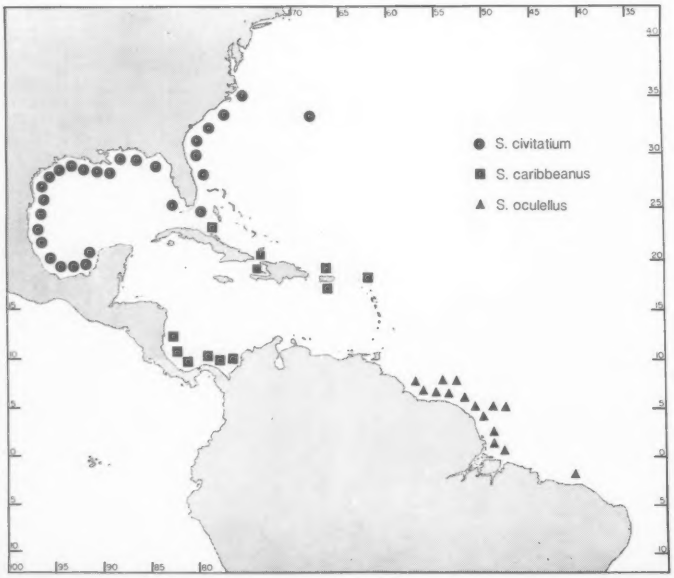
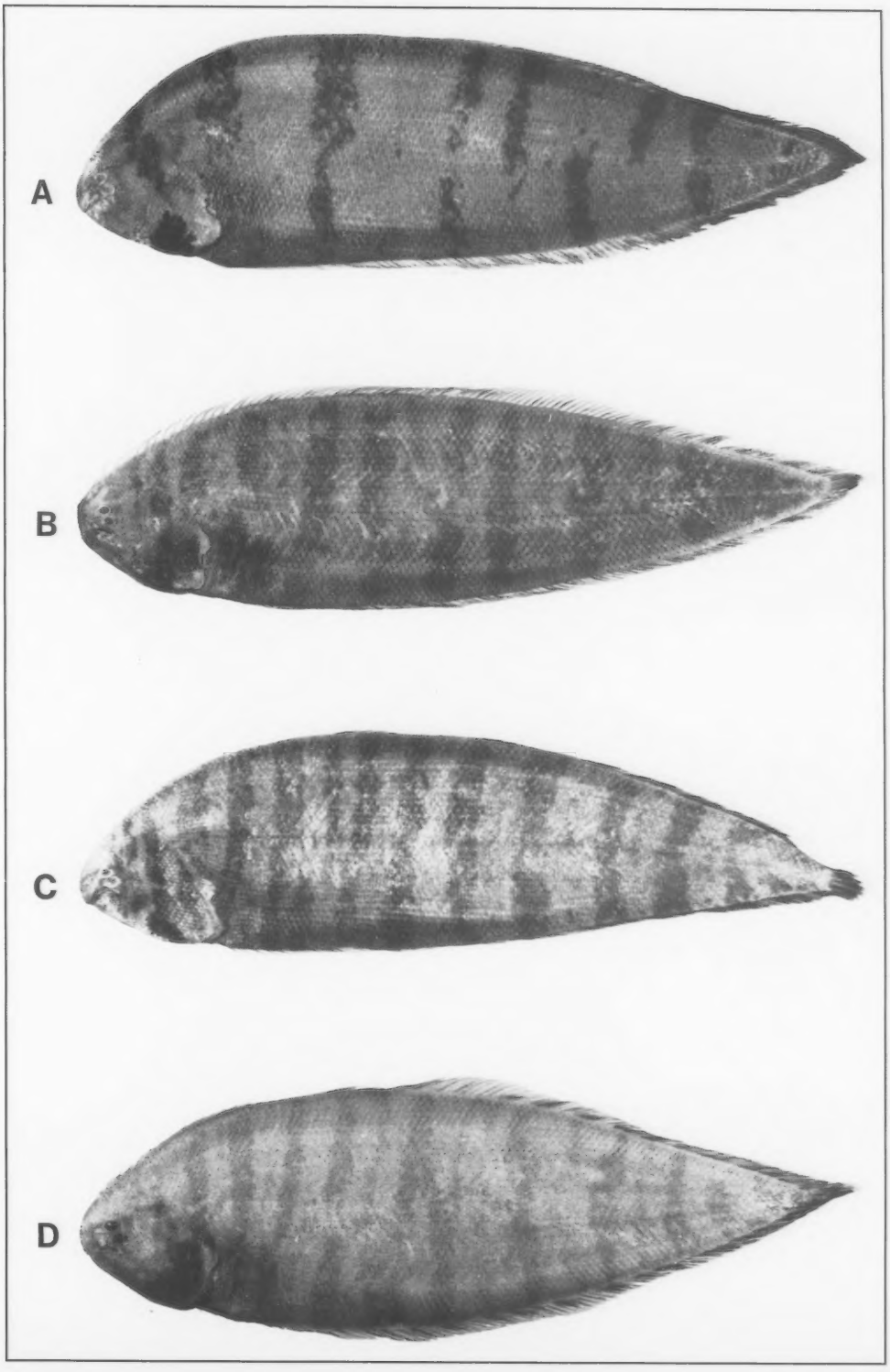



**Figure 5**
Geographic distributions of *Symphurus civitatium*, *S. oculellus*, and *S. caribbeanus* based on material examined.

**Figure 6 (facing page)**
(A) *Symphurus tessellatus*, USNM 159536, Female, 177 mm SL, Surinam, 6°41′N, 54°17′ W. (B–C) *Symphurus oculellus*. (B) Holotype, USNM 159606, 144 mm SL, Male, 6°24′N, 55°00′W; (C) USNM 313515, 151 mm SL, Female, 6°21′N, 54°28′W. (D) *Symphurus caribbeanus*, Holotype, USNM 313487, 101 mm SL, Male, Mayaguez Bay, Puerto Rico.


A
B
C
D

## Systematics

### *Symphurus plagusia* (Schneider, in Bloch and Schneider 1801) Figures 1a, 2, 3, 4a

#### Synonymy

*Plagusia* Browne 1756 (Jamaica; non-binomial; suppressed (Opinion 89 [Hemming and Noakes 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956).

*Pleuronectes plagusia* Browne 1789:445 (Jamaica; non-binomial; suppressed (Opinion 89 [Hemming and Noakes 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956). Cuvier 1816:224 (listed). Cuvier 1829:344 (listed).

*Pleuronectes plagusia* Schneider, in Bloch and Schneider 1801:162 (after Browne; no original material examined, based strictly on description provided by Browne).

?*Achirus ornata* (*nomen dubium*) Lacepède 1802:659, 663 (vague description of a tonguefish donated to France by Holland but of uncertain identity and geographic origin).

*Aphoristia ornata*. Kaup 1858:107 (in part) (new combination; synonymized with *Plagusia tessellata* Quoy and Gaimard 1824). Günther 1862:490 (in part) (synonymy; meristics; synonymized with *Plagusia tessellata* Quoy and Gaimard 1824). Poey 1868:409 (in part) (synonymy; listed, Cuba). Poey 1876:182 (in part) (synonymy; listed, Cuba). Goode and Bean 1885:196 (in part) (substitute name for *Pleuronectes plagiusa* Linnaeus 1766). Jordan 1885:395 (in part) (possible synonymy of *A. ornata* Lacepède 1802 with *Pleuronectes plagiusa* Linnaeus 1766; *Aphoristia ornata* Lacepède 1802 from Jamaica distinct from *A. fasciata* [= *Plagusia fasciata*] Holbrook in DeKay 1842).

*Aphoristia plagiusa* (not of Linnaeus). Jordan 1886a: 31 (Cuba; equals *A. ornata* of Poey). Jordan 1886b: 603 (in part) (West Indies; equals *A. ornata* of Poey).

*Symphurus plagusia*. Jordan and Goss 1889:100 (in part) (synonymy, nomenclature review; West Indies to Brazil; comparison with *S. plagiusa*; synonymized with *Plagusia tessellata* Quoy and Gaimard 1824). Jordan and Evermann 1898:2709 (in part) (synonymy, counts, measurements, description; after Jordan and Goss). Meek and Hildebrand 1928:1005 (in part) (synonymy; counts, measurements, description; summary of distribution records; listed, Panama). Chabanaud 1939:26 (listed, Antilles). Chabanaud 1940: 182 (descriptive osteology). Chabanaud 1949:82 (synonymy; description including counts, measurements, description of scales; figures; radiograph; mouth of Amazon, Brazil). Duarte-Bello and Buesa 1973:234 (in part) (synonymy; listed, Cuba). Menezes and Benvegnú 1976:142 (in part) (recommended reexamination of Ginsburg's diagnoses of two subspecies). Rosa 1980:222 (in part) (listed, nearshore and estuarine habitats, Paraiba, Brazil). Lema et al. 1980:44 (in part) (synonymy; listed, southern Brazil).

*Symphurus plagusia plagusia*. Ginsburg 1951:199 (in part) (synonymized with *Plagusia tessellata* Quoy and Gaimard 1824; description and diagnoses of two subspecies; four species included in material studied). Carvalho et al. 1968:22 (in part) (brief description; in key; Antilles, Central America to Brazil). Palacio 1974:87 (in part) (counts; suggested reexamination of subspecies status; listed, Colombia). Lema and Oliveira 1977:6 (in key; suggested synonymy of *Pleuronectes plagusia*, *Plagusia tessellata*, and *Symphurus civitatium*). Soares 1978:23 (in part) (listed, northern Brazil).

**Diagnosis** A *Symphurus* with the following combination of characters: predominant ID pattern 1-4-3; 12 caudal fin rays; unpigmented peritoneum; fleshy ridge on ocular-side lower jaw; no pupillary operculum; relatively small, spherical eye (64–95 HL, $\bar{x}$ 82); 89–97 dorsal fin rays; 73–81 anal fin rays; 47–51, usually 49–50, total vertebrae; 79–89 scales in longitudinal series; moderately long jaws, usually extending posteriorly to vertical line through posterior margin of lower eye, less frequently to vertical through rear margin of pupil or slightly posterior to rear margin of lower eye; dorsal fin origin placed far forward, usually at vertical through anterior margin of upper eye, or with first and sometimes second rays inserting anterior to vertical through anterior margin of upper eye; scales absent on blind sides of dorsal and anal fin rays; ocular surface usually uniformly light-brown or yellowish, occasionally with 8–14 narrow, faint crossbands; outer surface of ocular-side opercle without black blotch, pigmentation usually same as that of body (some specimens with dusky blotch on upper opercular lobe as a consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus dusky- to dark-brown, that of blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin. Dorsal and anal fins uniformly pigmented, without progressive darkening or alternating series of pigmented blotches and unpigmented areas posteriorly.

**Description** A medium-sized tonguefish attaining maximum known body sizes of approximately 130 mm SL. ID pattern usually 1-4-3 (32/42 individuals), less frequently 1-3-3 (4), 1-4-2 (2), or 1-3-4 (1) (Table 1). Caudal fin rays 12(39/42), infrequently 11 or 13 (Table

**Table 9**

Summary of morphometrics, expressed as thousandths of standard length (except SL in mm) for the neotype (ANSP 132030) and 14 non-type specimens of *Symphurus plagusia*. (Abbreviations defined in Methods section.)

| Character | Neotype | Range | Mean | SD |
|---|---|---|---|---|
| SL | 103.2 | 57.4–130.3 | 98.8 | 22.29 |
| BD | 304 | 278–319 | 292.1 | 13.05 |
| PDL | 30 | 23–50 | 32.9 | 6.87 |
| PAL | 222 | 166–244 | 209.3 | 18.60 |
| DBL | 970 | 950–977 | 967.1 | 6.87 |
| ABL | 776 | 758–802 | 785.6 | 15.38 |
| PL | 64 | 51–73 | 63.6 | 5.76 |
| PA | 48 | 38–60 | 50.0 | 7.00 |
| CFL | 98 | 88–111 | 100.3 | 7.13 |
| HL | 196 | 174–216 | 189.6 | 11.98 |
| HW | 239 | 218–256 | 236.4 | 13.25 |
| POL | 130 | 110–143 | 125.9 | 9.26 |
| SNL | 45 | 36–54 | 43.3 | 4.21 |
| UJL | 42 | 38–52 | 43.1 | 4.56 |
| ED | 16 | 12–18 | 15.3 | 2.02 |
| CD | 42 | 39–67 | 52.1 | 7.99 |
| UHL | 142 | 125–186 | 160.1 | 15.93 |
| LHL | 107 | 81–115 | 96.8 | 10.22 |

**Table 10**

Summary of morphometrics expressed as thousandths of head length (except HL and HW) for the neotype (ANSP 132030) and 14 non-type specimens of *Symphurus plagusia*. (Abbreviations defined in Methods section.)

| Character | Neotype | Range | Mean | SD |
|---|---|---|---|---|
| HL/HW | 1.2 | 1.2–1.3 | 1.2 | 0.38 |
| POL | 663 | 630–714 | 665.8 | 25.18 |
| SNL | 228 | 205–250 | 229.1 | 15.62 |
| UJL | 213 | 200–250 | 227.6 | 14.99 |
| ED | 79 | 64–95 | 81.9 | 9.57 |
| CD | 213 | 222–374 | 275.1 | 40.32 |
| OPLL | 272 | 250–346 | 296.9 | 29.10 |
| OPUL | 223 | 169–272 | 211.9 | 27.24 |
| UHL | 703 | 695–926 | 843.1 | 63.80 |
| LHL | 530 | 427–606 | 510.3 | 53.23 |

2). Dorsal fin rays 89–97 (Table 3). Anal fin rays 73–81 (Table 4). Total vertebrae 47–51, usually 49–50 (32/42 specimens) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 79–89 (Table 6). Scale rows on head posterior to lower orbit 18–22, usually 18–20 (Table 7). Transverse scales 35–43 (Table 8).

Proportional measurements appear in Tables 9 and 10. Body relatively deep (278–319 SL, $\bar{x}$ 292); maximum depth in anterior one-third of body. Preanal length 166–244 SL, $\bar{x}$ 209; shorter than body depth. Head relatively short (174–216 SL, $\bar{x}$ 190) and wide (HW 218–256 SL, $\bar{x}$ 236); usually much wider than long (HW/HL 1.2–1.3, $\bar{x}$ 1.2); lower head lobe relatively narrow (81–115 SL, $\bar{x}$ 97) considerably narrower than upper head lobe (125–186 SL, $\bar{x}$ 160). Lower opercular lobe of ocular side considerably wider (250–346 HL, $\bar{x}$ 297) than upper opercular lobe (169–272 HL, $\bar{x}$ 212). Postorbital length 110–143 SL, $\bar{x}$ 126. Snout moderately long (205–250 HL, $\bar{x}$ 229), somewhat square (Fig. 4a), covered with small ctenoid scales. Anterior nostril not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind side of snout and chin regions. Jaws moderately long, upper jaw length 200–250 HL, $\bar{x}$ 228; posterior extension of maxilla usually reaching to vertical line through posterior margin of lower eye, less frequently only to vertical through rear margin of pupil or slightly posterior to rear margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4a). Chin depth 222–374 HL, $\bar{x}$ 275. Lower eye small (64–95 HL, $\bar{x}$ 82), spherical; upper eye usually anterior to lower eye; eyes not covered with scales; usually 1–2 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 950–977 SL, $\bar{x}$ 967. Dorsal fin origin placed far forward (Fig. 4a), usually at vertical through anterior margin of upper eye or with first and sometimes second fin rays inserting anterior to vertical through anterior margin of upper eye; predorsal length 23–50 SL, $\bar{x}$ 33. Length of anal fin base 758–802 SL, $\bar{x}$ 786. Scales absent on blind sides of dorsal and anal fin rays. Pelvic fin length 51–73 SL, $\bar{x}$ 64; longest pelvic fin ray reaching base of first or occasionally second anal fin ray; pelvic to anal fin distance 38–60 SL, $\bar{x}$ 50. Posterior pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in many specimens). Caudal fin length moderate (88–111 SL, $\bar{x}$ 100).

Teeth well developed on blind-side jaws. Ocular-side dentary without teeth or with short row of small teeth developed only on anterior one-half to one-third; premaxilla on ocular side usually with small, single, mostly incomplete row of slender teeth anterior to vertical equal with anterior nostril.

Scales large, ctenoid on both sides of body.

**Pigmentation** Ocular surface usually uniformly light-brown or yellowish, occasionally with 8–14 narrow, faint crossbands. Crossbands not continued onto dorsal and anal fins; mostly complete in anterior trunk region; on remainder of body obvious only as vertical markings at body margin along dorsal and anal fin bases.

**Table 11**
Bathymetric distribution (meters) for five species of the western Atlantic *Symphurus plagusia* complex. Numbers represent the percent occurrence of individuals.

| | | Depth | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | *N* | 1–10 | 11–20 | 21–30 | 31–40 | 41–50 | 51–60 | 61–70 | 71–80 | 81–90 | 110 |
| *civitatium* | 216 | 2 | 26 | 34 | 26 | 5 | 5 | 0.5 | 0.5 | | |
| *tessellatus* | 349 | 10 | 26 | 2 | 24 | 19 | 5 | 8 | 6 | 0.3 | |
| *oculellus* | 57 | 4 | 19 | 12 | 9 | 9 | 2 | 40 | — | 4 | 2 |
| *plagusia* | 25 | 80 | — | — | 16 | — | — | 4 | | | |
| *caribbeanus* | 94 | 51 | 32 | 17 | | | | | | | |

Blind side creamy-white. Peritoneum unpigmented. Pigmentation of outer surface of ocular-side opercle usually same as that of body; occasionally with dusky blotch on upper opercular lobe due to pigment on inner lining of ocular-side opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually dusky; some specimens with dark-brown pigmentation on inner opercular lining; inner opercle and isthmus on blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin. Usually with slight pigment band on ocular-side upper lip and diffuse pattern of melanophores on lower lip.

Dorsal and anal fins dusky; fin rays streaked with pigment darker brown than that of connecting membrane; sometimes with alternating series of darker-pigmented rays (usually 2–3 in succession) separated by about 4–5 successive, lighter-pigmented rays. Basal half (scale-covered) of caudal fin dark-brown; fin rays in distal half streaked with pigment.

**Size and sexual maturation** (Fig. 2) *Symphurus plagusia* is a medium-sized tonguefish. The largest of five males examined was 130 mm SL; the largest of 23 females was only slightly smaller (127 mm SL).

Sexual maturity occurs at a relatively large body size in this species. All females larger than 80 mm SL were mature. All but one female (79.3 mm SL) smaller than 80 mm SL were immature, with gonads undergoing elongation without ripening ova or with ovaries barely elongating.

**Geographic distribution** (Fig. 3) Widely distributed in shallow waters of the tropical western Atlantic. In the northern portion of its distribution, this species occurs in Puerto Rico, Haiti, and Hispaniola, but is unknown from the Bahamas (Böhlke and Chaplin 1968). Along the continental margin of Central America, *S. plagusia* has been collected at Belize, Nicaragua, Costa Rica, and Panama, while further south it ranges along the Atlantic coast of Colombia and coastal regions in Surinam, Tobago, and Brazil at least as far south as Rio de Janeiro.

**Bathymetric distribution** *Symphurus plagusia* is a shallow-water species (1–51 m) most commonly inhabiting depths between the shoreline and 10 m (Table 11), where (20/25, 80%) of specimens examined were taken. All life-history stages occur in these shallow areas and only occasionally were individuals taken at deeper locations (one specimen at 51 m, three specimens at 40 m, and one specimen at 37 m).

**Ecology** Little is known concerning the biology of *S. plagusia*. Its general rarity in collections indicates that it occurs in rarely-sampled habitats.

**Remarks** The earliest description of a western Atlantic, shallow-water, 12-caudal-rayed tonguefish is of a specimen collected in Jamaica that Browne first described (1756) as *Plagusia* and later (1789) as *Pleuronectes plagusia*. He described this specimen as a small sinistral flatfish with dorsal, anal, and caudal fins united (tail ending in sharp point), lacking pectoral fins and lateral lines. His description was clearly that of a tonguefish, but he provided no figure or diagnostic characters to unequivocally identify his specimen. Browne's names were later suppressed under the plenary powers for nomenclatorial purposes in Opinion 89 of the Commission for Zoological Nomenclature (see Hemming and Noakes 1958).

In 1801, Schneider first made Browne's tonguefish *Pleuronectes plagusia* available as a binomial. Schneider's *Pleuronectes plagusia* was based entirely on the description of the tonguefish from Jamaica in Browne's works (1756, 1789). The description by Schneider (in Bloch and Schneider 1801) is identical to that provided by Browne and, in addition, all indications are that Schneider did not directly examine any specimens of this species. Dr. H.-J. Paepke (Mus. für Naturkunde der Humboldt-Universität zu Berlin, Zoologisches Mus., Invalidenstrasse 43, Berlin DDR 1040, pers.

commun. 8 Nov. 1986) informs me that no remarks were made in Bloch's ledger to indicate that specimens were available for examination when Schneider wrote the description of *Pleuronectes plagusia*. Additionally, Paepke also stated that there are no specimens of this species in the Bloch and Schneider collection. Therefore, it appears that the description of *Pleuronectes plagusia* Schneider, in Bloch and Schneider 1801, was copied directly from Browne's work and that no type exists for this species.

Although quite vague, the original description of *Pleuronectes plagusia* by Schneider does refer to a species of *Symphurus* and is the oldest available name for a tropical, western Atlantic species in the genus. This name represents the oldest binomial generally considered to represent a member of this species group and has been the one name most consistently applied to any shallow-water tonguefish possessing 12 caudal fin rays. In order to stabilize the nomenclature for this species, it is necessary to designate a neotype. Since the original description is based on a specimen from Jamaica, a topotypic specimen would be the most appropriate neotype. Unfortunately, no specimens of *S. plagusia* from Jamaica were available to Munroe (1987) and several more recent attempts to procure a specimen during the present study have also been unsuccessful. All tonguefishes collected from Jamaican waters that I have examined are specimens of *S. tessellatus* trawled at depths generally exceeding those usually occupied by *S. plagusia*. Therefore, designation of a neotype for *S. plagusia*, based on a topotype specimen from Jamaica, is not possible. Instead, ANSP 132030, a mature female measuring 103.2 mm SL, collected by beach seine at Puerto Yabucoa, Puerto Rico, 24–27 July 1974, is selected as the neotype for this species. Meristic features for this specimen are: ID pattern 1-4-3; caudal fin rays 12; dorsal fin rays 93; anal fin rays 78; total vertebrae 50; longitudinal scales 79; transverse scale count 39; and 18 scale rows on head posterior to eyes.

Many authors have included *Achirus ornatus* Lacepède 1802 in the synonymy of *Symphurus plagusia*. The description of this species is very brief and does not include figures or locality data, and it is unknown if any type(s) exists. The information provided is that the fish was donated to France by Holland, and has the following characteristics: dorsal and anal fins joined, 95 dorsal fin rays, 82 anal fin rays, 8 or 9 dark transverse bands, and a lateral line on each side. Notably absent in Lacepède's account is the caudal-fin-ray count for this specimen. The lateral line referred to in the description may refer to the mid-lateral junction of the myomeres that is apparent on some tonguefish specimens (especially those partially dehydrated during preservation). Based on counts listed by Lacepède, it is possible his specimen is a *S. plagusia* (*sensu strictu*). However, the dark, transverse bands and meristic features listed in the description of *Achirus ornatus* could also apply to several other western Atlantic tonguefishes. Among shallow-water species possessing 12 caudal fin rays, the data fit at least three species: *S. caribbeanus* (described below), *S. plagusia* (Schneider, in Bloch and Schneider 1801), and *S. tessellatus* (Quoy and Gaimard 1824). Of these, the description is more typical of *S. tessellatus*, especially the reference to darkly-pigmented crossbands. Nonetheless, the exact identity of *Achirus ornatus* Lacepède cannot be determined from the vague original description, particularly given the unknown site of capture for the specimen on which this name is based. *Achirus ornatus* Lacepède 1802 is therefore regarded as a *nomen dubium*.

In 1824, Quoy and Gaimard described *Plagusia tessellata* from Rio de Janeiro Bay (= Guanabara Bay), Brazil. Although no figure of this specimen was provided, the descriptive account of meristic features, color pattern, and other characters leave little doubt as to the identity of the species. Quoy and Gaimard described the dorsal fin as originating above the eyes and consisting of 99 rays; the anal fin has 78 rays. The color is described as brown with small transverse bands of the same color. Although no type exists for this species (M.L. Bauchot, Ichtyologie Générale et Appliquée, 43 Cuvier, Mus. Natl. Hist. Nat., Paris Cedex 05 75231, pers. commun. 23 June 1982), the original description is sufficient to allow identification of this species. Unfortunately, most authors beginning with Kaup (1858) and continuing to Ginsburg (1951) regarded this species as a junior synonym of *S. plagusia* (Schneider, in Bloch and Schneider 1801). It is unlikely that the specimen described by Quoy and Gaimard belongs to *S. plagusia* (*sensu strictu*), because the *S. tessellatus* specimen has slightly higher meristic features, darker banding, and the dorsal fin origin is described as being above and not anterior to the eyes, which is the typical condition found in *S. plagusia*.

A second nominal species of tonguefish from Brazilian waters, *Plagusia brasiliensis*, described by Agassiz (in Spix and Agassiz 1829–1831), has also been placed in the synonymy of *S. plagusia*. The possible holotype or syntype (MHNN 691; see Kottelat 1984, 1988) was illustrated and an adequate description provided. The specimen has 99 dorsal fin rays, 83 anal fin rays, 12 caudal fin rays, 53 total vertebrae, several small ctenoid scales on the blind sides of the dorsal and anal fin rays, the dorsal fin origin at the vertical through the front margin of the pupil of the upper eye, and a relatively large eye (10.6% HL). It agrees in all these features with *S. tessellatus* and is removed from the synonymy

of *S. plagusia* and placed in the synonymy of *S. tessellatus* (see below).

Beginning with Kaup (1858), all previously described species of western Atlantic, shallow-water tonguefishes possessing 12 caudal fin rays were regarded as a single species. Kaup placed *Achirus ornatus* Lacepède, *Plagusia brasiliensis* Agassiz, in Spix and Agassiz (Kaup cited authorship of this species as Cuvier, in Spix), and *Plagusia tessellatus* Quoy and Gaimard (Kaup listed Valenciennes as the author of this name) in synonymy and proposed the new combination *Aphoristia ornata* to accommodate a single, widespread species ranging from the Caribbean to southern South America. Günther (1862) regarded *Aphoristia ornata* as including the nominal species *Pleuronectes plagusia* Browne, *Plagusia brasiliensis* Agassiz, and *Plagusia tessellatus* Quoy and Gaimard.

Subsequent authors, including Jordan and Goss (1889) and Jordan and Evermann (1898), until Ginsburg (1951), continued to include three species in the synonymy of *Symphurus* (= *Aphoristia*) *plagusia* (Schneider, in Bloch and Schneider): *P. tessellatus*, *P. brasiliensis*, and *A. ornatus*. Jordan and his co-workers, and other researchers, still recognized only one widespread, polytypic species of shallow-water, 12-caudal-rayed *Symphurus* occurring in the western Atlantic. Ginsburg (1951), although continuing to regard all Caribbean and South American specimens as representing a single widespread, polytypic species, *S. plagusia* (Schneider, in Bloch and Schneider 1801), allocated his study specimens to two allopatric subspecies. He considered *S. plagusia plagusia* as a northern subspecies ranging from the West Indies to Central America that was characterized by somewhat lower meristic features. The second subspecies, *S. p. tessellatus*, with a more southern distribution along the coasts of Brazil and Uruguay had higher meristic features. In this revision, Ginsburg also described a second species (*S. civitatum* = *civitatium*, this study) of shallow-water, 12-caudal-rayed tonguefish from continental seas off the southeastern United States and Gulf of Mexico. He equivocated in his description of this new species, stating that his *S. civitatium* could also be recognized as a third northern subspecies of a widespread, polytypic *S. plagusia*.

Subsequent workers have utilized subspecies designations proposed by Ginsburg for Caribbean and South American shallow-water, 12-caudal-rayed tonguefishes and have used the name *S. civitatium* for specimens collected in the Gulf of Mexico and along the southeastern coast of the United States. More recently, however, several studies have noted that both nominal subspecies of *S. plagusia* occur sympatrically in northern South America. For example, Carvalho et al. (1968) found both subspecies in northern Brazil, and Palacio (1974) reported both subspecies from the Colombian Caribbean.

In their revision of western South Atlantic tonguefishes, Menezes and Benvegnú (1976) reported that all their specimens (collected mostly in offshore habitats by trawling) were quite similar, lacking variation reported for specimens collected in more northern regions. Using the name *S. plagusia*, they considered their specimens to represent a single taxon but also pointed out that the sympatric occurrence of both subspecies in other South American localities indicated that the subspecific status designated by Ginsburg should be reexamined.

In examining material of *S. plagusia*, I successfully located 19 of the 25 specimens listed by Ginsburg (1951) in his account of *S. plagusia plagusia*. These include representatives of four species: twelve *S. tessellatus*, one *S. caribbeanus*, one *S. parvus* Ginsburg 1951, with only five actually *S. plagusia* (*sensu strictu*). The twelve specimens of *S. tessellatus* incorrectly identified as *S. p. plagusia* by Ginsburg are small juveniles collected from shallow-water habitats. These, as well as many of the remaining 25 specimens that Ginsburg included in his account of *S. p. plagusia*, had been collected in the latter part of the last century and during the early 1920s. Most of these older specimens were completely devoid of any obvious pigmentation pattern. As a consequence, the specimens provided little clue that more than a single species was represented in these shallow-water collections. Additionally, since most of Ginsburg's Caribbean and Central American specimens came from shallow-water collections, very few adult *S. tessellatus* were available to his study. Therefore, he was unable to unravel size-related differences among the three sympatric species in this complex that occur in this region (the two smaller species, *S. plagusia* and *S. caribbeanus*, and the much larger *S. tessellatus*).

Ginsburg did not list catalog numbers for 34 specimens identified as *S. p. tessellatus* in his study, so that it is difficult to ascertain if more than one species was included in his account of this subspecies. Of the eight lots designated as *S. p. tessellatus* by Ginsburg that I have examined, all are one species, *S. tessellatus* (Quoy and Gaimard 1824). It is highly probable, therefore, that Ginsburg's *S. p. tessellatus* are equivalent to *S. tessellatus* (Quoy and Gaimard 1824) in the present study.

**Comparisons** *Symphurus plagusia* most closely resembles *S. civitatium* but differs from that species in its modally higher meristic features (total vertebrae modally 49–50 vs. 47–49 in *S. civitatium*; dorsal fin rays 89–97 vs. 86–93; anal fin rays 73–81 vs. 70–78); and degree of development of sexually dimorphic coloration. In *S. plagusia*, both sexes are more or less

uniformly pigmented with only slight evidence of banding on the body, and with vertical fins of both sexes uniformly colored with no darkening in the posterior portion of the body. In contrast, in *S. civitatium* there is considerably more pronounced sexual dimorphism in pigmentation. Females tend to have well-developed crossbands on the body whereas in males the crossbands are less conspicuous. In male *S. civitatium*, posterior portions of the dorsal and anal fins are noticeably darkened with black pigment (black pigment absent in females).

*Symphurus plagusia* of all sizes are usually collected with juveniles and small adults of *S. tessellatus*. Despite overall similarities in meristic features, the two species are quite distinctive. *Symphurus plagusia* is uniformly colored with only faint, narrow crossbands in some individuals, has a well-developed fleshy ridge on the ocular-side lower jaw (Fig. 4a), and this species lacks a striking black pigment spot on the outer opercle (some individuals have a diffuse blotch on the inner opercle where the pigmentation on the inner surface of the ocular-side opercle shows through). In *S. tessellatus*, in contrast, all individuals have a bold pattern of wide crossbands, a prominent black spot on the outer surface of the opercle, and lack a fleshy ridge on the ocular-side lower jaw (Fig. 4c). *Symphurus plagusia* also has a smaller eye (6.4–9.5, $\bar{x}$ 8.2% HL vs. 7.9–11.4, $\bar{x}$ 9.5% HL in *S. tessellatus*) and lacks the small ctenoid scales on the posterior fin rays on the blind side of the dorsal and anal fins that are present in *S. tessellatus* larger than about 70 mm SL. *Symphurus plagusia* also has modally lower meristic values (total vertebrae 49–50 vs. 50–53 in *S. tessellatus*; dorsal fin rays 89–97 vs. 91–102 (usually 93–101); anal fin rays 73–81 vs. 77–86 in *S. tessellatus*).

*Symphurus plagusia* differs further from *S. tessellatus* in the almost squarish snout of *S. plagusia*, which contrasts with the more pointed snout of *S. tessellatus* (compare Figs. 4a and 4c). Also, in *S. plagusia* the dorsal fin origin is usually anterior to the vertical through the eye, while in *S. tessellatus* the dorsal fin originates slightly more posteriorly, usually above the anterior margin of the pupil of the upper eye, or even as far back posteriorly as the mid-eye region. Viewed from the blind side, the more posterior location of the dorsal fin origin in *S. tessellatus* is apparent in the number of rays occurring along the dorsal margin of the body immediately above the space between the two nostrils. In *S. tessellatus* usually only the first dorsal fin ray occurs above the space between the nostrils, while the second dorsal fin ray lies immediately above the posterior nostril or the second dorsal fin ray is placed even slightly posterior to the rear nostril. In *S. plagusia*, usually the first two dorsal fin rays occur along the dorsal margin in the space between the nostrils, and in many specimens the first dorsal fin ray is actually situated anterior to the vertical equal with the anterior nostril. In *S. plagusia*, the jaws usually extend to the posterior margin of the lower eye or, in some cases, actually extend slightly posterior to the rear margin of the lower eye, while in *S. tessellatus* the jaws usually reach only to the middle, rarely to the posterior margin, of the lower eye.

These two species also differ significantly in overall body size and size at sexual maturation. *Symphurus plagusia* is a medium-sized tonguefish reaching a maximum known body size of about 130 mm SL and attaining sexual maturity as small as 80 mm SL. *Symphurus tessellatus* is a much larger species attaining maximum known lengths of 220 mm SL and does not attain sexual maturity until reaching approximately 120 mm SL.

Meristic values of *S. plagusia* overlap almost completely those of *S. caribbeanus*. The two species can be distinguished, however, by the absence in *S. caribbeanus* of the fleshy ridge on the ocular-side lower jaw (present in *S. plagusia*; see Figures 4a and 4e). *Symphurus plagusia* is generally uniformly colored with only slight evidence of crossbanding, and the fins are uniformly colored. In contrast, *S. caribbeanus* usually has numerous, prominent crossbands on the body, and the vertical fins have an alternating series of blotches and unpigmented areas, which are especially well developed posteriorly. *Symphurus caribbeanus* has a more pointed snout with a distance between upper eye and dorsal fin base usually slightly less than twice the eye diameter, versus a squarish snout with distance from upper eye to dorsal fin base usually larger than twice the eye diameter in *S. plagusia* (compare Figures 4a and 4e). The body shape of *S. caribbeanus* is rounded with a pronounced taper posterior to dorsal fin rays 25–35 (versus somewhat elongate in *S. plagusia* with a more gradual taper). Additionally, *S. caribbeanus* has a slightly larger eye (8.2–11.0% HL, usually 9.0–10.0% HL) when compared with that of *S. plagusia* (usually 7.0–9.0% HL).

*Symphurus plagusia* is also similar to *S. oculellus* with respect to small eye size and presence of a fleshy ridge on the ocular-side lower jaw. It differs from this species, however, in its much lower counts (47–51 total vertebrae vs. 52–55 in *S. oculellus*; dorsal fin rays 89–97 vs. 99–104; anal fin rays 73–81 vs. 82–88) and pigmentation pattern. *Symphurus plagusia* has a relatively uniform body color with faint crossbands, uniformly pigmented fins without blotches, and no pigment spot on the outer opercle (versus sharply contrasting crossbands, pigmented blotches alternating with unpigmented areas in the dorsal and anal fins, and a black spot on the outer opercle in *S. oculellus*). Furthermore, in *S. plagusia* the first, and occasionally the second, rays of the dorsal fin are usually located along

a vertical line anterior to the upper eye, while in *S. oculellus* the dorsal fin origin usually extends anteriorly only to the vertical through the anterior margin or mid-eye region of the upper eye. Differences in morphometrics between the two species are that *S. oculellus* has a narrower body (231–297 SL vs. 278–319 SL in *S. plagusia*) and attains larger sizes (up to 190 mm SL vs. largest of only 131 mm SL in *S. plagusia*).

Some meristic values of *S. plagusia* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus plagusia* occurs sympatrically, and occasionally syntopically, with *S. diomedeanus* (Goode and Bean) but differs from this species in having 12 caudal fin rays (versus 10 in *S. diomedeanus*) and in lacking the series of dark spots on posterior rays of the dorsal and anal fins and the pupillary operculum that are present in *S. diomedeanus*.

*Symphurus plagusia* can be distinguished from *S. plagiusa* (Linnaeus), which has an allopatric distribution in the western North Atlantic, in having 12 versus 10 caudal fin rays, and *S. plagusia* also lacks the well-developed black pigment spot on the ocular-side outer opercle (present in *S. plagiusa*). In addition, only the ocular-side opercular lining is pigmented in *S. plagusia* whereas the inner opercular linings on both sides of the body are heavily pigmented in *S. plagiusa*. *Symphurus plagiusa* has larger eyes (83–126 HL vs. 64–95 HL in *S. plagusia*) that are usually equal in position (slightly subequal in *S. plagusia*). Also, in *S. plagiusa* the jaws reach only as far posteriorly as a vertical through the mid-eye region; in contrast, in *S. plagusia* the jaws reach a vertical through the rear margin of the pupil or the rear margin of the eye, or the jaws occasionally even extend slightly beyond the vertical through the posterior margin of the lower eye in *S. plagusia*. In larger (>60 mm SL) *S. plagiusa*, there are 4–8 ctenoid scales on the blind sides of the dorsal and anal fin rays (scales usually absent altogether, or occasionally 1–2 scales along bases of fin rays in *S. plagusia*).

*Symphurus plagusia* is not easily confused with other Atlantic species (*S. kyaropterygium* Menezes and Benvegnú, *S. trewavasae* Chabanaud, *S. normani* Chabanaud, *S. piger* (Goode and Bean), *S. nigrescens* Rafinesque, *S. pusillus* (Goode and Bean), *S. lubbocki* Munroe, and *S. reticulatus* Munroe) with which it overlaps in meristic features. *Symphurus plagusia* differs from all of these in its 1-4-3 ID pattern (versus 1-4-2 in *S. kyaropterygium*; 1-3-3 in *S. trewavasae* and *S. normani*; 1-3-2 in *S. piger*, *S. nigrescens*, *S. pusillus*, *S. reticulatus*, and *S. lubbocki*). In addition, *S. plagusia* differs from the South Atlantic *S. kyaropterygium* in caudal-fin-ray number (12 vs. 10) and in lacking the pupillary operculum and dark pigment blotch on the caudal extremity that are present in *S. kyaropterygium*. It differs from the South Atlantic *S. trewavasae* in its caudal-fin-ray count (12 vs. 10) and smaller eye (64–95 HL vs. 114–162 HL in *S. trewavasae*). *Symphurus plagusia* lacks scales on the blind sides of the dorsal and anal fin rays and the spotted peritoneum that are present in *S. normani*. *Symphurus plagusia* differs from the 1-3-2 species (except *S. lubbocki* and *S. reticulatus*) in lacking a black peritoneum. *Symphurus plagusia* differs from *S. lubbocki* and *S. reticulatus* in having no dentition or greatly reduced dentition on ocular-side jaws (versus ocular-side jaws with complete or nearly complete row of teeth in *S. lubbocki* and *S. reticulatus*), its much larger size (130 vs. <50 mm SL), and pigmentation (dark- or light-brown, usually without crossbands, and with uniformly-pigmented fins, versus light-brown or yellowish body with incomplete crossbands in *S. lubbocki*, and dark, chocolate-brown body with X- and Y-shaped markings and vertical fins with alternating series of blotches and unpigmented areas in *S. reticulatus*).

Meristic values of *S. plagusia* overlap those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including *S. leei* Jordan and Bollman, *S. atricaudus* (Jordan and Gilbert), *S. melanurus* Clark, *S. williamsi* Jordan and Culver, *S. fasciolaris* Gilbert, and *S. melasmatotheca* Munroe and Nizinski. Of these species, *S. plagusia* is most similar to *S. melanurus* in that both species possess a fleshy ridge on the ocular-side lower jaw, and in both the first dorsal fin ray reaches a vertical equal with or anterior to the anterior margin of the upper eye. The two species are distinguished in that *S. plagusia* lacks a pupillary operculum (versus a weakly-developed pupillary operculum usually present in *S. melanurus*), has fewer scales in a longitudinal series (79–89 vs. 89–108 in *S. melanurus*), has a lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blind-side opercle in *S. melanurus*), and in *S. plagusia* the posterior dorsal and anal fins and the caudal fin are not darker than the anterior regions (versus progressive darkening in posterior dorsal and anal fins and darkly-pigmented caudal fin in *S. melanurus*). *Symphurus plagusia* differs from the remaining five eastern Pacific species with comparable meristic values in lacking a pupillary operculum (present in the others) and in having a fleshy ridge on the ocular-side lower jaw (absent in the others). *Symphurus plagusia* is further distinguished from *S. fasciolaris* and *S. melasmatotheca* in possessing 12 caudal fin rays (versus 10 and 11 in *S. fasciolaris* and *S. melasmatotheca*, respectively) and in lacking an ocellated spot on the caudal fin (present in *S. fasciolaris*) or pigmented peritoneum (present in *S. melasmatotheca*). *Symphurus plagusia* differs further from *S. atricaudus* and *S. williamsi* in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in these other species).

From *S. leei*, *S. plagusia* is further distinguished in having the head length considerably smaller than the head width (versus head length usually equal to or greater than head width in *S. leei*), in having a smaller eye (12–18 SL vs. 22–27 SL in *S. leei*), and in having an unpigmented peritoneum (versus black or heavily spotted in *S. leei*).

**Material examined** 45 specimens (19.5–130 mm SL).

**Counted and measured** (15 specimens, 57.4–130.3 mm SL) **Puerto Rico**: ANSP 132030; Neotype; (102.9); Puerto Yabucoa, one-half mile east of Playa de Guayanes, Municipio de Yabucoa; collected by J.J. Loos, 24–27 Jul 1973. FMNH 3286; (83.1); Mayaguez; 20 Jan 1899. FMNH 61572; (117.0); Allasco Bay; 10 Jan 1954. UF 12059; (127.1); beach at Mani, just N of Mayaguez; 16 Apr 1964. **Costa Rica**: UF 10762; (79.6); Tortuguero Lagoon, Limon Province; Aug 1963. **Panama**: GCRL 15694; (57.4); Canal Zone; 8 Feb 1977. **Trinidad**: UPRM 1828; (89.4); Icacos Bay; 4 May 1964. **Brazil**: FMNH 88853; 2(120.0–130.3); 2°09′S, 42°44′W; 40 m; 10 Mar 1963. UFPB 884; (101.4); Praiade Jacare; 13 Nov 1981. UFPB 896; 3(79.3–87.5); Rio Paraiba do Norte; 30 Jul 1981. ANSP 121326; 2(112.9–118.3); Atafona (23°02′S, 44°01′W); Jul–Aug 1963.

**Counted** (27 specimens, 17 lots) **Puerto Rico**: ANSP 118542; (47.4); Puerto Yabucoa; 25 Jan 1971. ANSP 129952; (112.7); Puerto Yabucoa; 21 Jul 1973. ANSP 129985; (98.2); Puerto Yabucoa; 25 Jul 1973. USNM 50178; 4(61.9–83.1); Ponce; 31 Jan 1899. **Haiti**: UF 33896; 5(82.8–90.8); 2 km NW of Port Salut; sandy beach near eelgrass bed; 7 Apr 1979. **Belize**: FMNH 97492; (49.3); Belizean Beach, 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97493; 2(52.1–68.2); Belizean Beach, 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97494; (25.1); Belize City, St. John's College Beach; 16 Apr 1973. FMNH 97495; (36.4); Belize City, St. John's College Beach, mangroves and beach; 3 Aug 1973. **Honduras**: FMNH 94818; (54.3); Brus Lagoon; 1 m; 10 May 1975. FMNH 94822; (34.8); Roatan; 1 m; 1 May 1975. FMNH 97490; 3(19.5–61.3); Stann Creek District, along Pelican Beach, 17–33 m N of Pelican Beach Motel; 30 Mar 1973. FMNH 97491; (40.0); Stann Creek District, along Pelican Beach, 17–33 m N of Pelican Beach Motel; 15 Apr 1973. **Panama**: UMML 34347; (121.5); 7°42′N, 57°32′W; 27 m; 15 Jul 1968. USNM 81654; (54.9); Colon; 5 Jan 1911. **French Guiana**: USNM 236252; (110.5); 6°34′N, 54°28′W; 37 m; 28 Jun 1972. USNM 291331; (79.4); 5°30′N, 52°10′W; 51 m; 12 Sep 1958.

**Other material examined** (3 specimens, 1 lot) **Tobago**: USNM 313648; 3(19.5–20.3); Bloody Bay, 11°18′14″N, 60°37′46″W; 3 m; 13 Sep 1990.

## *Symphurus civitatium* Ginsburg 1951
## Figures 1b–c, 2, 4b

### Synonymy

*Symphurus piger* (not of Goode and Bean). Baughman 1950:137 (inner harbor, Freeport, Texas).

*Symphurus civitatum* Ginsburg 1951:198 (counts, figure, included in key; Gulf of Mexico and southeastern coasts of the United States; see "Remarks" about emendation of specific name). Springer and Bullis 1956:65 (Gulf of Mexico; list of *Oregon* stations at which this species was collected). Resén-dez 1979:646 (occurrence in lagunas El Carmen, La Machona, and Lagunade Terminos, northern Mexico).

*Symphurus civitatus*. Briggs 1958:297 (summary of distribution records; North Carolina to Florida and widespread in Gulf of Mexico; see "Remarks" about emendation of specific name). Roithmayr 1965:22 (included in industrial bottomfish catch in north-central Gulf of Mexico). Struhsaker 1969:298 (rarely occurring [<10% of the tows] in demersal fish community of continental shelf from North Carolina to central Florida). Swingle 1971:65 (listed, offshore waters of Alabama). Topp and Hoff 1972:78 (general absence from west Florida shelf). Miller and Jorgenson 1973:305 (meristic features reported for four specimens). Chittenden and McEachran 1976: 93; 99 (abundance on continental shelf of northwestern Gulf of Mexico). Walls 1976:390 (counts, figure, in key; suggested synonymy with *S. plagiusa*). Schwartz et al. 1981:32 (Cape Fear River, North Carolina). McCaffrey 1981:204 (in part) (abundance and distribution in northeastern Gulf of Mexico). Darcy and Gutherz 1984:104 (collected on west Florida continental shelf).

**Diagnosis** *Symphurus civitatium* is identified by the combination of: a predominant 1-4-3 ID pattern; 12 caudal fin rays; an unpigmented peritoneum; absence of a pupillary operculum; relatively small eye (70–110 HL, $\bar{x}$ 88); a fleshy ridge on the ocular-side lower jaw; 86–93 dorsal fin rays; 70–78 anal fin rays; 46–50, usually 47–49 total vertebrae; 66–83, usually 74–82, scales in longitudinal series; relatively short jaws usually extending posteriorly to a vertical line through the middle of the pupil of the lower eye, or sometimes extending to the vertical line through the posterior margin of the pupil of the lower eye; dorsal fin origin usually situated at the vertical anterior to the front margin of the upper eye, or occasionally only reaching the vertical line through the front margin of the pupil of the upper eye; scales usually absent on the blind sides of the dorsal and anal fin rays (occasionally with 1–3 small scales at proximal bases of fin rays but without scales on distal portions of fin rays); ocular surface

usually light- to dark-brown, occasionally with 6–14 narrow, dark-brown crossbands; outer surface of ocular-side opercle without black blotch, pigmentation usually same as that of body (some specimens with dusky blotch on upper opercular lobe as a consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus usually heavily pigmented, that of blind side usually unpigmented. Dorsal and anal fins considerably darker posteriorly, without an alternating series of pigmented blotches and unpigmented areas.

**Description** A medium-sized tonguefish reaching maximum lengths of approximately 152mm SL. The usual ID pattern (Table 1) is 1-4-3 (127/177 specimens), less frequently 1-4-2 (19/177) and 1-5-2 (7/177). Caudal fin rays usually 12 (163/171), infrequently 11 (Table 2). Dorsal fin rays 86–93 (Table 3). Anal fin rays 70–78 (Table 4). Total vertebrae 46–50, usually 47–49 (170/174) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 66–83, usually 74–82 (Table 6). Scale rows on head posterior to lower orbit 16–20, usually 17–19 (Table 7). Transverse scales 26–39, usually 31–38 (Table 8).

Proportional measurements appear in Tables 12 and 13. Body relatively deep (247–328 SL, $\bar{x}$ 307) with greatest depth in anterior one-third of body. Preanal length 147–238 SL, $\bar{x}$ 202. Head moderately short, 170–219 SL, $\bar{x}$ 191; considerably shorter than body depth. Head wide (212–271 SL, $\bar{x}$ 238); usually greater than head length (HW/HL 1.0–1.5, $\bar{x}$ 1.2); lower head lobe (87–118 SL, $\bar{x}$ 104) narrower than upper head lobe (139–184 SL, $\bar{x}$ 159). Lower opercular lobe of ocular side (253–388 HL, $\bar{x}$ 321) considerably wider than upper opercular lobe (178–329 HL, $\bar{x}$ 230). Postorbital length 117–187 SL, $\bar{x}$ 134. Snout relatively short (169–231 HL, $\bar{x}$ 206), somewhat square (Fig. 4b); covered with small ctenoid scales. Anterior nostril, when depressed posteriorly, not reaching anterior margin of lower eye. Dermal papillae well developed on blind side of snout and chin regions. Jaws relatively short; upper jaw length 181–289 HL, $\bar{x}$ 228; posterior extension of maxilla usually reaching to vertical line through middle of pupil of lower eye or sometimes to vertical through posterior margin of pupil of lower eye. Chin depth 225–331 HL, $\bar{x}$ 268. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4b). Lower eye relatively small (70–110 HL, $\bar{x}$ 88); upper eye slightly anterior to lower eye; eyes not covered with scales; usually only 1–3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 925–982 SL, $\bar{x}$ 963. Dorsal fin origin (Fig. 4b) usually situated at vertical line anterior to front margin of upper eye; occasionally dorsal fin origin only reaching vertical line through front margin of pupil of upper eye; predorsal length 22–46 SL, $\bar{x}$ 34. Scales usually absent on blind sides of dorsal and anal fin rays; occasionally with 1–3 small scales at proximal bases of fin rays but without scales on distal portions of fin rays. Pelvic fin length 49–85 SL, $\bar{x}$ 63; longest pelvic fin ray usually reaching base of first or occasionally second anal fin ray; pelvic to anal fin distance 33–74 SL, $\bar{x}$ 45. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 87–124 SL, $\bar{x}$ 109.

Teeth well developed on blind-side jaws. Dentary on ocular side with single, mostly incomplete row of slender teeth on anterior one-third of jaw. Premaxilla on ocular side with only short row of teeth on anterior one-third; or occasionally lacking teeth altogether.

Scales large, ctenoid on both sides of body.

**Pigmentation** Body coloration generally similar for both sexes (dichromatic differences in pigmentation are discussed below). Ocular surface light- to dark-brown; sometimes with dark-brown crossbands continuous across the body. Crossbands, when developed, narrow, 6–14 in number, sometimes sharply contrasting (especially in mature females), otherwise faint and barely perceptible against dark body coloration. Crossbands not continued onto dorsal and anal fins. First band

**Table 12**

Summary of morphometrics expressed in thousandths of standard length, except SL (in mm), for the holotype (USNM 155227) and 29 additional specimens of *Symphurus civitatium*. (Abbreviations defined in Methods section.)

| Character | Holotype | *N* | Range | Mean | SD |
|---|---|---|---|---|---|
| SL | 110.3 | 30 | 48.8–149.3 | 108.6 | 24.96 |
| BD | 304 | 30 | 247–328 | 306.9 | 16.42 |
| PDL | 43 | 29 | 22–46 | 34.5 | 6.78 |
| PAL | 210 | 30 | 147–238 | 202.4 | 19.75 |
| DBL | 957 | 30 | 925–982 | 963.0 | 13.22 |
| ABL | 787 | 30 | 745–891 | 797.9 | 31.36 |
| PL | 68 | 30 | 49–85 | 63.0 | 8.83 |
| PA | 39 | 26 | 33–74 | 44.7 | 10.23 |
| CFL | 124 | 29 | 87–124 | 108.6 | 9.32 |
| HL | 200 | 30 | 170–219 | 191.3 | 11.55 |
| HW | 240 | 30 | 212–271 | 238.3 | 14.42 |
| POL | 134 | 30 | 117–187 | 134.3 | 13.64 |
| SNL | 41 | 30 | 31–47 | 39.5 | 3.55 |
| UJL | 54 | 30 | 37–54 | 43.5 | 4.88 |
| ED | 16 | 30 | 13–21 | 16.6 | 2.01 |
| CD | 62 | 29 | 39–68 | 50.6 | 7.32 |
| UHL | 159 | 30 | 139–184 | 158.9 | 11.60 |
| LHL | 103 | 30 | 87–118 | 103.9 | 6.86 |

**Table 13**
Summary of morphometrics expressed in thousandths of head length (except HW/HL) for the holotype (USNM 155227) and 29 additional specimens of *Symphurus civitatium*. (Abbreviations defined in Methods section.)

| Character | Holotype | *N* | Range | Mean | SD |
|---|---|---|---|---|---|
| HW/HL | 1.2 | 30 | 1.0–1.5 | 1.2 | 0.10 |
| POL | 670 | 30 | 645–740 | 692.0 | 27.45 |
| SNL | 204 | 30 | 169–231 | 206.4 | 13.84 |
| UJL | 272 | 30 | 181–289 | 227.7 | 24.14 |
| ED | 81 | 30 | 70–110 | 87.8 | 10.26 |
| CD | 308 | 29 | 225–331 | 267.9 | 30.55 |
| OPLL | 371 | 29 | 253–388 | 321.3 | 34.80 |
| OPUL | 217 | 29 | 178–329 | 230.0 | 34.86 |
| UHL | 792 | 30 | 636–996 | 832.6 | 82.14 |
| LHL | 516 | 30 | 462–629 | 543.0 | 46.00 |

crossing head short distance anterior to opercular opening. Crossbands along trunk 3–6 scale rows wide. Two posteriormost bands immediately anterior to caudal fin base often conjoined. Blind side off-white. Peritoneum unpigmented. Dorsal margin of outer surface of ocular-side opercle often with dusky blotch due to dark pigmentation of inner lining of opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually heavily pigmented; lining of blind-side opercle and blind-side isthmus usually unpigmented. Band of pigmentation usually developed on ocular-side upper lip; lower lip on ocular side frequently spotted but usually without definite band.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. All dorsal and anal fin rays on anterior two-thirds of body streaked with brown pigment similar in shade and intensity to body color. Fin rays completely pigmented other than for extreme distal tips, which are unpigmented. Membranes of anterior three-fourths of fins unpigmented. Caudal fin and dorsal and anal fins on posterior one-third of body more heavily pigmented and considerably darker than anterior two-thirds of fin. Fin membranes on posterior quarter of body heavily pigmented. Basal one-third of caudal fin more lightly pigmented than posterior two-thirds of fin. Distal tips of middle caudal fin rays unpigmented, or with tips of middle caudal fin rays streaked with pigment but membrane unpigmented.

**Size and sexual maturity** (Fig. 2) The largest fish examined, a female (152 mm SL), was only slightly larger than the largest male (149 mm SL). Most specimens examined ranged in size from 80 to 140 mm SL.

Females mature at sizes usually larger than 90 mm SL. Of 86 females examined, only three (83–95 mm SL) were immature. The two smallest gravid females were 80–90 mm SL, whereas the majority of gravid females were usually larger (91–140 mm SL).

**Geographic distribution** (Fig. 5) Western North Atlantic from Cape Hatteras, North Carolina, to the Yucatan Peninsula of Mexico. There is a single record for this species from Bermuda (ANSP 137573). In the Gulf of Mexico, *S. civitatium* occurs most commonly west of Apalachicola Bay in northern Florida (Springer and Bullis 1956, Chittenden and McEachran 1976, McCaffrey 1981). It is one of the most commonly collected tonguefishes on inner continental shelf regions in the central and western portions of the Gulf of Mexico from Alabama to Texas. Along northern Mexico, this species occurs coastally on sandy substrates at least as far south as coastal lagoons (lagunas El Carmen y La Machona, Laguna de Terminos) in Tabasco and Campeche, Mexico (Reséndez 1979) and on the continental shelf of the southern Gulf of Mexico (Cabo Rojo, Veracruz to Sabuncuy, Yucatan).

Collection data for 347 specimens from this study reveal a general absence of this species from the western Florida shelf. Only two collections record this species from the Tortugas region off southern Florida. Topp and Hoff (1972) also noted the general absence of this species along the west Florida shelf and found just a single record for *S. civitatium* in the eastern Gulf of Mexico (St. Joseph Bay; from Ginsburg 1951). Neither their efforts during the Hourglass cruises on the continental shelf off west Florida nor other studies (Moe and Martin 1965, Ogren and Brusher 1977, Naughton and Saloman 1978) have collected this species in coastal and continental shelf habitats off west Florida. Furthermore, Darcy and Gutherz (1984) reported taking only a single specimen during 338 10-minute bottom trawls in 9–193 m on the west Florida shelf.

*Symphurus civitatium* occurs on sand or silt substrates throughout its range. The geographic and bathymetric distribution of this species apparently coincides with the distribution of terrigenous, quartzite sandy, and silty substrates on the inner continental shelf. The scarcity of this species on the west Florida shelf and Yucatan Peninsula may reflect the strikingly different substrate compositions there. Along the west Florida shelf, primarily in depths of 55–92 m, Topp and Hoff (1972) reported that substrates consist of lithified sediments of cemented lime, including (1) nearshore deposits of cemented shell beachrock, (2) limestone, ranging from soft marl to conglomeritic and foraminiferal limestone, (3) small patches of living and dead coral, and (4) calcareous algae. They noted that substrates off the Yucatan Peninsula are similar in composition to those of the west Florida shelf. In

contrast, in the central and western Gulf of Mexico from the Mississippi Delta to Cabo Rojo, Veracruz, where *S. civitatium* is very abundant, substrates on the inner shelf consist largely of terrigenous quartzite sands, silts, and clays delivered primarily by Mississippi and Rio Grande rivers (van Andel 1960).

Substrate preference may also affect the distribution of *S. civitatium* in coastal seas off the southeastern United States. The depth of occurrence (11–40 m, see below) for *S. civitatium* apparently coincides with sand-silt substrates on the inner portions of the shelf, and this species is absent from live-bottom habitats occurring at similar depths (Struhsaker 1969).

The specimen of *S. civitatum* reported by Lazzaro (1977:69) from the continental shelf off Uruguay is neither this species nor any other of the *Symphurus plagusia* complex (those possessing 12 caudal fin rays, a 1-4-3 ID pattern, and an unpigmented peritoneum). The body shape evident in the photograph, meristic features, and great depth of occurrence (183 m) indicate the specimen is probably *S. ginsburgi* Menezes and Benvegnú.

**Bathymetric distribution** Although *S. civitatium* has been collected over a wide depth range of 1–73 m (Table 11), its center of abundance, based on overall frequency of capture and general abundance, occurs between 11 and 45 m. Approximately 91% (199/216) of the specimens examined in the present study were captured at these depths. The deepest captures were at 73 and 62 m, where a single fish was taken each time. It is unusual for adult *S. civitatium* to occur in shallow, inshore regions. Of four fish collected shallower than 10 m, three were small juveniles (<35 mm SL). Recently, several small juveniles (22–24 mm SL) have been collected in the Cape Fear River estuary, North Carolina (S.W. Ross, Dep. Nat. Resour., Morehead City, NC, pers. commun. 24 July 1985). It is not known how regularly this species occurs in these inshore areas or whether the recent captures represent isolated occurrences; however, Schwartz et al. (1981) listed this species as rare in the Cape Fear River estuary. Seasonal occurrence and abundance of juveniles in nearshore waters need further investigation.

McCaffrey (1981) reported capture depths of 30–187 m for 23 specimens purported to be *S. civitatium* taken on the continental shelf in the northeastern Gulf of Mexico between 84°30′ and 89°00′W longitudes. Nineteen of these specimens were collected between 80 and 187 m, depths considerably deeper than records for specimens I examined. Not all specimens identified as *S. civitatium* by McCaffrey were preserved and curated in collections (at least nine were indicated as having been discarded). One retained specimen (UF 70946) collected at 45 m, is *S. civitatium*, but two other specimens (UF 70885) from *Tursiops* Station 7019-07 with an estimated depth of 187 m are, rather, *S. pusillus* (Goode and Bean) and an undescribed species (species C of Munroe 1987), which occur commonly at depths similar to that reported for this station (187 m). Given the complexity of the series identified as *S. civitatium* in McCaffrey's study, the very deep captures reported (80–187 m) for *S. civitatium* are probably erroneous.

**Remarks** In the original description of *S. civitatum*, Ginsburg (1951:198) stated that this species and *S. plagusia* differed enough to consider them distinct species but that it was possible that they represented subspecies of a more widespread polytypic species. It was shown earlier (see "Remarks" section in account of *S. plagusia*) that Ginsburg had more than one species in his account of *S. plagusia*, and therefore his subspecific designations for this species were unfounded. *Symphurus civitatium* is consequently recognized as a species within this complex of morphologically similar species of *Symphurus*.

The etymology of the name *civitatum*, applied by Ginsburg to this species, is unclear from the original description. The name may have been derived from the genitive plural of *civitas* (meaning "of the citizenry"). Following this assumption, the proper genitive plural is *civitatium*, not *civitatum* as indicated by Ginsburg (G.C. Steyskal, Dep. Entomology, Natl. Mus. Nat. Hist., Wash. DC, pers. commun. 1989). Thus, the spelling of the specific name for this species remains unchanged regardless of generic assignment of the species. Therefore, spelling changes such as *S. civitatus* (Bailey et al. 1960, and other checklists of common and scientific names) are incorrect.

**Comparisons** *Symphurus civitatium* is most similar to, but has a completely allopatric distribution from, the Caribbean and South Atlantic species *S. plagusia*. Differences between these two species were discussed in the "Comparisons" section under the account for *S. plagusia*.

Meristic features of *S. civitatium* overlap at least partially those of two other Atlantic species belonging to this complex (the Caribbean and South Atlantic species *S. caribbeanus* and *S. tessellatus*). There is almost complete overlap in several meristic features between *S. civitatium* and *S. caribbeanus*; however, *S. civitatium* has a fleshy ridge on the ocular-side lower jaw (absent in *S. caribbeanus*; see Figures 4b and 4e) and has lower modal counts for total vertebrae (47–49 vs. 49–50 in *S. caribbeanus*), dorsal fin rays (86–93 vs. 89–96), and anal fin rays (70–78 vs. 74–80). *Symphurus civitatium* also has narrow crossbands with uniformly-colored fins (becoming progressively darker

in the posterior portions of sexually mature males). In contrast, *S. caribbeanus* has numerous well-developed crossbands and vertical fins with an alternating series of blotches and unpigmented areas in individuals of both sexes. *Symphurus caribbeanus* also has a more pointed snout with only a narrow space between the upper eye and dorsal fin base (versus a square snout with a space between the upper eye and the dorsal fin base usually greater than twice the eye diameter in *S. civitatium*; compare Figures 4b and 4e).

Despite some overlap in certain meristic values, *S. civitatium* and *S. tessellatus* are quite distinctive. The easiest way to distinguish these species is that *S. civitatium* has a well-developed fleshy ridge on the ocular-side lower jaw (absent in *S. tessellatus*; compare Figures 4b and 4c), lacks a black spot on the ocular-side opercle, and, when present on the body, crossbands are faint and narrow, whereas *S. tessellatus* has a bold pattern of wide crossbands and a well-developed black opercular spot. Other distinctions between these species include the absence of scales on the blind sides of the dorsal and anal fin rays of *S. civitatium* (present in *S. tessellatus* larger than about 60 mm SL), fewer vertebrae (total vertebrae 47–49 vs. 50–53 in *S. tessellatus*), and modally lower meristic features: dorsal fin rays 86–93 vs. 91–102 (usually 93–101) in *S. tessellatus*; anal fin rays 70–78 vs. 77–86; scales in a longitudinal series 66–83 vs. 81–96.

Some meristic values of *S. civitatium* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus civitatium* occurs sympatrically with *S. diomedeanus* and *S. plagiusa* and may be collected with these species. The suggestion by Walls (1976:390) to synonymize *S. civitatium* with *S. plagiusa*, based on partial overlaps in meristic features, pigmentation, and ecological co-occurrence, is not supported by results of this study. *Symphurus civitatium* differs from both these species primarily in caudal-fin-ray count (12 vs. 10 in the others) and by notable differences in pigmentation patterns. *Symphurus diomedeanus* usually has a series of black spots on posterior rays of the dorsal and anal fins and a well-developed pupillary operculum (both characters absent in *S. civitatium*). *Symphurus civitatium* can be distinguished from *S. plagiusa* in that *S. plagiusa* usually has a well-developed black spot on the outer surface of the ocular-side opercle (absent altogether or only a diffuse blotch resulting from pigment from the inner opercular lining showing to the outside in *S. civitatium*), and inner opercular linings on both sides are heavily pigmented (only the ocular-side opercular lining is pigmented in *S. civitatium*). *Symphurus plagiusa* has larger eyes (83–126 HL) that are usually equal in position (versus smaller eyes 70–110 HL, which are slightly subequal in position in *S. civitatium*). Also, the jaws reach only as far posteriorly as a vertical through the mid-eye region in *S. plagiusa*, while in *S. civitatium* the jaws reach a vertical through the rear margin of the pupil, the rear margin of the eye, or may even extend slightly beyond a vertical equal with the posterior margin of the lower eye in *S. civitatium*. In larger *S. plagiusa*, there are 4–8 ctenoid scales on the blind sides of the dorsal and anal fin rays (absent or at most only 1–2 scales along bases of fin rays in *S. civitatium*).

*Symphurus civitatium* is not easily confused with other Atlantic species (*S. kyaropterygium*, *S. trewavasae*, *S. normani*, *S. piger*, *S. nigrescens*, *S. pusillus*, *S. lubbocki*, and *S. reticulatus*) with which it overlaps in some meristic features. *Symphurus civitatium* differs from all of these in ID pattern (1-4-3 versus other patterns: 1-4-2 in *S. kyaropterygium*; 1-3-3 in *S. trewavasae* and *S. normani*; 1-3-2 in *S. piger*, *S. nigrescens*, *S. pusillus*, *S. reticulatus*, and *S. lubbocki*). In addition to differences in ID pattern, *S. civitatium* differs from the South Atlantic *S. kyaropterygium* in caudal-fin-ray number (12 vs. 10) and in lacking the pupillary operculum and darkly-pigmented blotch on the caudal extremity both present in *S. kyaropterygium*. *Symphurus civitatium* differs from the South Atlantic *S. trewavasae* principally in caudal-fin-ray count (12 vs. 10) and its smaller eye (70–110 HL vs. 114–162 HL in *S. trewavasae*). The eastern Atlantic *S. normani* possesses scales on the blind sides of the dorsal and anal fin rays, has a spotted peritoneum, and pepper-dot pigmentation on the blind side of the body (all absent in *S. civitatium*). *Symphurus civitatium* differs from the species with a 1-3-2 ID pattern (except *S. lubbocki* and *S. reticulatus*) in lacking a black peritoneum. *Symphurus civitatium* is further distinguished from *S. lubbocki* and *S. reticulatus* in having a fleshy ridge on the ocular-side lower jaw (absent in these others), in lacking complete dentition on ocular-side jaws (ocular-side jaws without dentition, or with only a partial row of teeth, versus ocular-side jaws with complete dentition in *S. lubbocki* and *S. reticulatus*), by its much larger size (152 vs. <50 mm SL), and by differences in pigmentation (dark-brown body with crossbands and uniformly-pigmented fins versus light-brown or yellowish body with incomplete crossbands in *S. lubbocki* and dark chocolate-brown body with X- and Y-shaped markings and vertical fins with alternating series of blotches and unpigmented areas in *S. reticulatus*).

Meristic values of *S. civitatium* overlap those of five eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. fasciolaris*, and *S. melasmatotheca*. Of these species, *S. civitatium* is most similar to *S. melanurus* in that both possess a fleshy ridge on the ocular-side lower jaw, and in both the first dorsal fin ray reaches the vertical equal with or anterior to the

anterior margin of the upper eye. The two species differ in that *S. civitatium* lacks a pupillary operculum (versus a weakly-developed pupillary operculum usually present in *S. melanurus*), has fewer scales in a longitudinal series (66–83 vs. 89–108 in *S. melanurus*), and *S. civitatium* has an unpigmented or only lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blind-side opercle in *S. melanurus*). *Symphurus civitatium* differs from the remaining four eastern Pacific species that have comparable meristic values in lacking a pupillary operculum (present in the others) and in having a fleshy ridge on the ocular-side lower jaw (absent in the others). *Symphurus civitatium* is further distinguished from *S. fasciolaris* and *S. melasmatotheca* in possessing 12 caudal fin rays (versus 10 and 11 in *S. fasciolaris* and *S. melasmatotheca*, respectively) and in lacking an ocellated spot on the caudal fin (present in *S. fasciolaris*) or pigmented peritoneum (present in *S. melasmatotheca*). *Symphurus civitatium* differs further from *S. atricaudus* and *S. williamsi* in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in these other species). From *S. leei*, *S. civitatium* is further distinguished in having the head length considerably smaller than the body depth (versus head length nearly equal with body depth in *S. leei*), in having a smaller eye (13–21 SL vs. 22–27 SL in *S. leei*), and in having an unpigmented peritoneum (versus black in *S. leei*).

**Material examined** 298 specimens (22.0–149.0 mm SL).

**Counted and measured** (30 specimens, 48.8–149.0 mm SL). **Southeastern United States. North Carolina**: USNM 157403; Paratype (109); 35°21′10″, 75°22′40″; 26 m; 19 Oct 1884. **Florida**: TU 75907; 3(131–136); 27°35′04″N, 80°04′04″W; 26 m; 5 Sep 1965. UF 13062; (130); 28°35.5′N, 80°08′W; 62 m; 21 Feb 1965. USNM 154946; Paratype (139); Cape Canaveral; 18 m; 4 Apr 1940. **Gulf of Mexico. Alabama**: ALA 3015; 3(75.5–85.2); to 30 m; 1968. **Mississippi**: ALA 606.29; (94.4); Horn Island; Jul–Aug 1958. FMNH 45979; (110); 29°22′N, 88°40′W; 51 m; 22 Oct 1953. **Louisiana**: USNM 155227; Holotype (110); 29°06′30″N, 89°40′W; 17 m; 8 Jul 1938. USNM 313647; 2(48.8–72.2); Calcasieu Lake (ca. 30°N, 93°W); Feb 1982. **Texas**: FMNH 45109; 3(138–149); 27°43′N, 96°51′W; 27 m; 26 Sep 1950. USNM 313646; 9(88.6–108); 3 mi. offshore, Port Aransas (ca. 28°N, 97°W); 15 m; 16 Sep 1982. **Mexico**: IMS 544; 3(121–130); W Campeche; 27 m; 22–29 Jul 1951. UMML 34365; (130); 20°12′N, 91°40′W; 37 m; 11 Dec 1952.

**Counted paratypes** (148 specimens, 41 lots). **Gulf of Mexico. Florida**: USNM 86153; (120); St. Joseph's Bay; 27 Jan 1917. **Alabama**: USNM 157402; (117); Mobile; 13 m; 7 Feb 1917. **Louisiana**: USNM 86140; (120); Calcasieu Pass; 9 m; 15 Feb 1917. USNM 154945; 3(122–130); 28°54′N, 91°41.5′W; 18 m; 11 Jul 1938. USNM 154947; 5(110–123); 28°55.5′N, 91°46′W; 18 m; 11 Jul 1938. USNM 154948; 2(120–124); 28°58′N, 91°40.5′W; 16 m; 12 Nov 1938. USNM 154949; 2(105–129); 28°41.5′N, 91°10′W; 15 m; 11 Nov 1938. USNM 154950; 2(122–124); 28°47′N, 91°21.5′W; 11 Jul 1938. USNM 154951; (126); 29°12′N, 89°50.5′W; 13 m; 8 Jul 1938. USNM 154952; (117); 28°43′N, 91°13′W; 15 m; 11 Jul 1938. USNM 154953; 2(102–105); 29°12.5′N, 89°57′W; 7 m; 10 Jul 1938. USNM 154954; 3(114–118); 28°35.5′N, 91°01.5′W; 22 m; 13 Jul 1938. USNM 155226; (114); 28°45′N, 91°17.5′W; 16 m; 11 Jul 1938. USNM 157399; 3(109–121); Grand Terre; 2 Jul 1930. USNM 157400; 3(99.7–118); Grand Terre; 27 Jun 1930. **Texas**: USNM 86139; 2(118–126); Aransas Pass; 15 m; 5 Mar 1917. USNM 120081; (111); Galveston; 1941. USNM 120082; (81.5); Aransas Pass; 7 Aug 1941. USNM 157401; (117); Galveston; 10 m; 26–27 Feb 1917.

**Counted (non-type material). Southeastern United States. Florida**: UMML 34342; 3(136–140); 28°34′N, 80°15′W; 42 m; 19 Nov 1964. USNM 274484; (117); 28°13.5′N, 80°21′W; 22 m; 14 Nov 1963. USNM 291316; (132.0); 28°13′N, 80°21′W; 22 m; 14 Nov 1963. USNM 291317; 13(114–142); 28°13′N, 80°21′W; 22 m; 14 Nov 1963. UMML 34343; (131); 28°12′N, 80°05′W; 60 m; 14 Mar 1965. UMML 34344; (118); 27°57′N, 80°03′W; 55 m; 28 Sep 1963. **Gulf of Mexico. Alabama**: ALA 301.17; 2(85.4–94.3); Dauphin Island; 28 Sep 1952. ALA 353.05; (108); Mobile Ship Channel; 6 Sep 1951. ALA 2385; 13(85.8–103); Dauphin Island; 15 Jul–20 Aug 1966. **Texas**: TCWC 4187.4; (100); 29°10′N, 94°30′W; 14 m; 28 Sep 1973. TCWC 4189.21; 18(97.8–124); 28°26′N, 95°23′W; 28 m; 29 Sep 1973. TCWC 4195.31; 9; 28°25 N, 95°18′W; 35 m; 31 Oct 1973. UMML 34345; (128); 28°07′N, 95°53′W; 37 m; 26 Jan 1958. **Mexico**: FMNH 45427; 7(126–140); 20°18′N, 91°48′W; 42 m; 7 Dec 1952. UMML 34366; (130); 20°12′N, 91°40′W; 37 m; 11 Dec 1952. USNM 157693; 5(117–126); 20°05′N, 91°28′W; 31 m; 26 Aug 1951. USNM 157694; 3(128–132); 20°05′N, 91°28′W; 31 m; 26 Aug 1951. USNM 291318; (127); Campeche, Yucatan, 20°05′N, 91°28′W; 31 m; 26 Aug 1951. FMNH 46369; 11(115–138); 19°48′N, 91°20′W; 25 Aug 1951. GCRL 16383; 2(76.0–86.5); Lagunas de Terminos, Punta Zachtal, Campeche; 17 Nov 1970. IMS 543; 16(126–142); Pta Frontera; 31 m; 29 Jul–6 Aug 1951. USNM 274485; (132); N of Soto La Marina; 15 Mar 1947.

**Other material examined** (120 specimens, 22 lots). **Bermuda**: ANSP 137573; (79.3); washed onto shore. **Southeastern United States. North Carolina**: 3(22-24); Cape Fear River; Aug 1981; (uncatalogued reference specimens, CP&L Biol. Lab., Southport, NC 28461). **Florida**: UF 35486; (125); 29°58.1′N, 81°16.9′W; 14 m. TU 92501; 25(82.0–120); 29°11′05″N, 80°53′05″W; 12 m; 24 Feb 1970. UMML 34346; 3(118–134); 28°22′N, 80°05′W; 60 m; 14 Mar 1965. **Gulf of Mexico. Florida**: ANSP 94305; (25.0); Key West; 1 m; 21 Mar 1958. **Mississippi**: FMNH 45980; 2(110–120); 28°45′N, 89°15′W; 60 m; 23 Oct 1953. FMNH 86369; (113); 29°42′N, 88°29′W; 37 m; 10 Aug 1951. TU 5374; 18(113–137); 29°14.4′N, 88°52.4′W; 32 m; 11 Aug 1952. TCWC 2251.1; (126); 29°09′N, 88°52′W; 73 m; 10–16 Dec 1963. **Alabama**: FMNH 89568; 2(119–121); 29°42′N, 88°29′W; 37 m; 10 Aug 1951. ALA 798.14; 2(108–110); Gulf Shores, Breton Island; 3 Aug 1959. UF 70946; (115); 29°41′N, 88°14.5′W; 45 m; 22 Jul 1971. USA 1905; 25(91.9–122); 29°57′N, 87°54′W; 26 m; 20 Apr 1975. **Louisiana**: ANSP 55825; (125); Breton Island; Nov 1930. BMNH 1931.11.5:75; 1; Reversed Specimen; Breton Island. FMNH 45981; 2(109–119); 28°56′N, 89°09′W; 59 m; 25 Oct 1953. **Texas**: CAS-SU 40556; (133.4); Freeport; 28 Apr 1940. FMNH 79851; 3(139–152); 27°43′N, 96°53′W; 26 m; 14 Dec 1950. UMMZ 199071; 5(46.0–57.3); 8–9 Apr 1939. USA 4070; 20(111–127); 10 mi. SSE Port Aransas; 3 Dec 1975. **Mexico**: GCRL 16384; (32.7); Laguna el Carmen, Tabasco; 2 Mar 1978.

## *Symphurus tessellatus* (Quoy and Gaimard 1824) Figures 2, 3, 4c, 6a

### Synonymy

*Plagusia tessellata* Quoy and Gaimard 1824:240 (counts and color description; Rio de Janeiro Bay [= Guanabara Bay], Brazil).

*Plagusia brasiliensis* Agassiz, in Spix and Agassiz 1831:89 (counts, color description, and figure; Bahia, Brazil). Castelnau 1855:79 (brief description and figure). Whitehead and Myers 1971:495 (nomenclature and dating of Spix and Agassiz's Brazilian Fishes). Kottelat 1984:150 (listed in type catalogue of MHNN). Kottelat 1988:79 (nomenclature and type status of species described in Spix and Agassiz's Brazilian Fishes).

*Aphoristia ornata*. Kaup 1858:106 (in part) (synonymy; listed, South America). Günther 1862:490 (in part) (synonymized with *S. plagusia* Schneider, in Bloch and Schneider 1801; brief description; counts; Atlantic coasts of tropical America). Kner 1865-67: 292 (listed, Rio de Janeiro, Brazil).

*Symphurus plagusia* (not of Schneider, in Bloch and Schneider). Jordan and Goss 1889:324 (in part) (synonymy; in key; brief description; nomenclature; West Indies to Rio de Janeiro, Brazil). Jordan and Evermann 1898:2709 (in part) (after Jordan and Goss 1989). Berg 1895:79 (in part) (Mar del Plata–Montevideo; counts include those for *S. jenynsi*). Thompson 1916:416 (in part) (after Jordan and Goss; counts, measurements, brief color description). Devincenzi 1920:135 (Río de la Plata; distinguished from *S. jenynsi*). Devincenzi 1924–26:281 (listed, Uruguay; counts). Meek and Hildebrand 1928:1005 (in part) (color description; counts; Panama). Puyo 1949:178 (in part) (French Guyana; figure, counts, color description). Lowe-McConnell 1962:694 (in part) (listed, British Guiana). Caldwell 1966:84 (collections from offshore localities, Jamaica). Menezes and Benvegnú 1976:142 (synonymized with *S. plagusia*). Soares 1978:23 (listed, Rio Grande do Norte, Brazil; counts, color description, and figure). Lema et al. 1980:44 (Río de la Plata region, Rio Grande do Sul, Brazil; synonymy). Rosa 1980:222 (in part) (listed, nearshore and estuarine habitats, Paraiba, Brazil). Lucena and Lucena 1982:56 (listed, collections in southern Brazil). Matsuura *in* Aizawa et al. 1983:463 (listed, French Guiana and Surinam; counts, measurements, color photograph).

*Aphoristia fasciata* (not of DeKay). Goode and Bean 1896:458 (in key and figured; Jamaica).

*Symphurus plagusia tessellata*. Ginsburg 1951:199 (diagnosis and description of subspecies from Brazil-Uruguay). Ringuelet and Aramburu 1960:91 (in key; figure; synonymy; listed, Argentina). Carvalho et al. 1968:22 (in part) (synonymy; in key; brief description; occurrence in northern Brazil). Lazzaro 1973: 247 (in key; distribution in southern Brazil and Uruguay). Palacio 1974:87 (listed, north of Puerto, Colombia). Lazzaro 1977:70 (in key). Lema and Oliveira 1977:7 (recorded from Santa Catarina, Brazil; in key; suggested that *S. civitatium*, *S. tessellatus*, and *S. plagusia* are geographic races of the same species).

*Symphurus plagusia plagusia* (not of Schneider, in Bloch and Schneider). Cervigon 1966:816 (listed, Venezuela; probably *S. tessellatus* based on high meristic features, color description, and large sizes reported). Palacio 1974:87 (in part) (Colombia; specimens listed as *S. p. plagusia* were misidentified).

*Symphurus pterospilotus* (not of Ginsburg). Lema and Oliveira 1977:7 (in part) (specimens misidentified).

**Diagnosis** A *Symphurus* with the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; distinct, dark-brown or black, almost spherical blotch on the outer surface of the ocular-side opercle; 4–8 small ctenoid scales on the blind sides of the dorsal and anal fin rays (best developed on fin rays in posterior one-third of body in specimens >70 mm SL); lacking a fleshy ridge on the ocular-side lower jaw; 91–102 dorsal fin rays; 77–86, usually 78–84, anal fin rays; 49–54, usually 50–53, total vertebrae; 81–96, usually 83–93, scales in a longitudinal series; moderately long jaws usually extending to the vertical line through the middle or posterior margin of pupil of lower eye; moderately-sized eye (79–114 HL, $\bar{x}$ 95) without pupillary operculum; dorsal fin origin reaching the vertical line through the anterior margin of the upper eye, or occasionally only reaching the vertical through the middle of the upper eye; ocular surface dark- to light-brown, with 5–9 well-developed, sharply contrasting, relatively wide, dark-brown crossbands on head and trunk; inner lining of opercle and isthmus heavily pigmented on both sides of body; dorsal and anal fins without an alternating series of pigmented blotches and unpigmented areas; anterior dorsal and anal fin rays usually streaked with brown pigment; fin rays and membranes of dorsal and anal fins on posterior two-thirds of body becoming progressively darker posteriorly; males with posteriormost regions of fins almost uniformly black, while in females, posterior portions of fins, although darker than anterior regions, usually dark-brown and not as intensively pigmented as in mature males.

**Description** A large tonguefish, attaining adult sizes to 220 mm SL. ID pattern (Table 1) usually 1-4-3 (170/231 specimens), less frequently 1-5-3 (14), 1-4-2

**Table 14**

Summary of morphometrics expressed as thousandths of standard length (except SL in mm) for *Symphurus tessellatus* (*N* 22) and the possible holotype (MHNN 691) of *Plagusia brasiliensis* (a junior subjective synonym). (Abbreviations defined in Methods section.)

| Character | Range | Mean | SD | *P. brasiliensis* |
|---|---|---|---|---|
| SL | 97.9–203 | 145.0 | 27.66 | 140.3 |
| BD | 247–312 | 280.2 | 18.82 | 262 |
| PDL | 32–48 | 41.7 | 4.48 | 32 |
| PAL | 181–227 | 204.7 | 10.58 | 217 |
| DBL | 952–968 | 958.3 | 4.48 | 968 |
| ABL | 771–876 | 798.0 | 22.90 | 793 |
| PL | 44–73 | 59.0 | 6.47 | 43 |
| PA | 27–56 | 41.5 | 6.01 | — |
| CFL | 72–118 | 90.9 | 10.36 | 88 |
| HL | 170–199 | 186.6 | 7.37 | 175 |
| HW | 193–247 | 218.6 | 15.58 | 209 |
| POL | 117–135 | 125.9 | 5.38 | 117 |
| SNL | 35–46 | 40.3 | 2.55 | 32 |
| UJL | 41–52 | 46.3 | 3.12 | 41 |
| ED | 15–21 | 17.6 | 2.04 | 18 |
| CD | 33–63 | 46.4 | 6.51 | 36 |
| UHL | 113–163 | 143.3 | 12.03 | 120 |
| LHL | 80–114 | 97.8 | 10.56 | 94 |

**Table 15**

Summary of morphometrics expressed as thousandths of head length (except HL and HW) for *Symphurus tessellatus* (*N* 22) and the possible holotype (MHNN 691) of *Plagusia brasiliensis* (a junior subjective synonym). (Abbreviations defined in Methods section.)

| Character | Range | Mean | SD | *P. brasiliensis* |
|---|---|---|---|---|
| HL/HW | 1.1–1.4 | 1.2 | 0.08 | 1.2 |
| POL | 593–723 | 674.9 | 25.07 | 669 |
| SNL | 196–231 | 215.7 | 9.25 | 184 |
| UJL | 222–278 | 248.1 | 15.58 | 237 |
| ED | 79–114 | 95.2 | 10.06 | 106 |
| CD | 173–322 | 245.0 | 31.85 | 204 |
| OPLL | 243–359 | 306.8 | 31.68 | — |
| OPUL | 161–252 | 205.7 | 24.03 | — |
| UHL | 682–891 | 774.2 | 56.18 | 690 |
| LHL | 422–593 | 523.1 | 46.26 | 539 |

(10), or 1-3-3 (8). Caudal fin rays usually 12 (207/224), less frequently 10,11, or 13 (Table 2). Dorsal fin rays 91–102 (Table 3). Anal fin rays 77–86, usually 78–84 (Table 4). Total vertebrae 49–54, usually 50–53 (228/233) (Table 5). Hypurals 4. Longitudinal scale rows 81–96, usually 83–93 (Table 6). Scale rows on head posterior to lower orbit 18–23, usually 20–22 (Table 7). Transverse scales 38–45 (Table 8).

Proportional measurements appear in Tables 14 and 15. Body relatively elongate, only moderately deep (247–312 SL, $\bar{x}$ 280); greatest depth usually occurring in anterior third of body. Preanal length 181–227 SL, $\bar{x}$ 205. Head relatively short (170–199 SL, $\bar{x}$ 187); considerably shorter than body depth. Head relatively wide (193–247 SL, $\bar{x}$ 219), wider than head length (HW/HL 1.1–1.4, $\bar{x}$ 1.2); lower head lobe (80–114 SL, $\bar{x}$ 98) narrower in width than upper head lobe (113–163 SL, $\bar{x}$ 143). Lower opercular lobe on ocular side (243–359 HL, $\bar{x}$ 307) greater in width than upper opercular lobe (161–252, $\bar{x}$ 206). Postorbital length 117–135 SL, $\bar{x}$ 126. Snout (Fig. 4c) moderately long and somewhat pointed (196–231 HL, $\bar{x}$ 216); covered with small ctenoid scales. Anterior nostril, when depressed posteriorly, not reaching anterior margin of lower eye. Dermal papillae well developed on blind side of snout and chin regions, but not particularly dense, occasionally extending onto ocular-side snout. Jaws moderately long; upper-jaw length 222–278 HL, $\bar{x}$ 248; posterior extension of maxilla usually reaching to the vertical through the middle or posterior margin of pupil of lower eye. Ocular-side lower jaw lacking a fleshy ridge near posterior margin (Fig. 4c). Chin depth 173–322 HL, $\bar{x}$ 245. Lower eye moderate in size (79–114 HL, $\bar{x}$ 95); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 952–968 SL, $\bar{x}$ 958. Dorsal fin origin (Fig. 4c) usually reaching to vertical line through anterior margin of upper eye, or occasionally only reaching vertical line through middle of upper eye; predorsal length 32–48 SL, $\bar{x}$ 42. Length of anal fin base 771–876 SL, $\bar{x}$ 798. Four to eight scales present on blind sides of dorsal and anal fin rays (best developed on fin rays in posterior third of body of specimens >70 mm SL). Pelvic fin length 44–73 SL, $\bar{x}$ 59; longest pelvic fin ray usually reaching base of first anal fin ray or occasionally falling short of that point; pelvic to anal fin distance 27–56 SL, $\bar{x}$ 42. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 72–118 SL, $\bar{x}$ 91.

Teeth well developed on blind-side jaws. Dentary on ocular side usually with single, mostly incomplete row of slender teeth; premaxilla on ocular side either with very short row of teeth anterior to vertical line equal with anterior nostril or lacking teeth altogether.

Scales large, strongly ctenoid on both sides of body.

**Pigmentation** General pattern of body pigmentation similar in both sexes at all sizes but usually more intense in sexually mature males. Males, especially those

in breeding condition (collected with gravid females), usually with more intense banding, dark-black fins, dark-black spot on ocular-side opercle, and, additionally, some specimens with irregularly-shaped, black pigment patches on posterior one-half of blind side of body. In contrast, mature females also with crossbands but less conspicuous than in males and with posterior portions of fins dark-brown but usually not black. Females lack black pigment patches on blind side observed in males.

Ocular-surface background pigmentation ranging from dark- to light-brown. Body usually with 5–9 (usually 5–7) well-developed, sharply contrasting, relatively wide, dark-brown crossbands on head and trunk. First two bands relatively consistent in position; first crossing head immediately posterior to eyes; second crossing body immediately behind opercular opening. Crossbands on trunk variable in number and degree of completeness, especially those between opercular opening and point about equal to two-thirds of trunk length. Males usually with 3–4 well-developed and lesser number of incomplete bands along trunk. Two posteriormost bands, just anterior to caudal fin base, slightly arched and usually darker than others on body. Blind side usually uniformly creamy-white; some mature males with irregular patches of black pigment on caudal one-third of blind side. Peritoneum unpigmented.

Outer surface of ocular-side opercle usually with distinct, dark-brown or black spot on ventral margin slightly forward of posterior margin of opercle. Opercular spot ranging from almost spherical to dorsoventrally-elongate black blotch covering most of lower opercle. Intensity of pigmentation in spot maximally developed in sexually mature adults. Inner linings of opercles and isthmus heavily pigmented on both sides of body. Pigment band well developed on ocular-side upper lip; ocular-side lower lip frequently spotted but without well-defined band.

Anterior dorsal and anal fin rays usually streaked with brown pigment, more heavily pigmented than connecting membranes. Fin rays and membranes of dorsal and anal fins on posterior two-thirds of body becoming increasingly darker posteriorly. Males with posteriormost regions of fins almost uniformly black, while in females, posterior portions of fins, although darker than anterior regions, usually dark-brown and not as intensively pigmented as in mature males.

**Size and sexual maturity** *Symphurus tessellatus* is one of the largest species in the genus and is the second largest Atlantic tonguefish species after *S. jenynsi* Evermann and Kendall (Ginsburg 1951, Menezes and Benvegnú 1976, Munroe 1987). Size-related life-history information is based on data from 385 fish. Males and females attain nearly similar sizes, but females are somewhat larger. The largest fish measured in this study was a female of 220 mm SL; the largest male measured 205 mm SL.

There were 214 males, 155 females, and 16 immature fish among material examined. There were 119 mature females ranging in size from 104 to 220 mm SL (Fig. 2). Based on reproductive stages for females, sexual maturity in this species occurs at sizes of 104–120 mm SL, but usually larger than 115 mm SL. Most mature females exceeded 140 mm SL, with only six smaller than 125 mm SL and two smaller than 110 mm SL present among fish examined. Twenty-six females of 49.5–119 mm SL were immature. The smallest of these, measuring 49.5 and 62.8 mm SL, had ovaries that were scarcely elongate. Other immature females, ranging from 68.6 to 119 mm SL, had only partially elongate ovaries with no indications of developing ova.

**Geographic distribution** (Fig. 3) A widespread tropical species, ranging in the north from the larger Caribbean Islands such as Cuba, Hispaniola, and Puerto Rico, southward to Uruguay. In the West Indies, adults and juveniles have frequently been taken in abundance at several localities, but the distribution of this species appears limited by the location of soft silt and mud sediments. These bottom types are more common on the larger islands that support river and estuarine habitats. The species has been taken at several inshore locations in Puerto Rico, Cuba, and Haiti, and a large number of adults were collected by the RV *Oregon* on the shelf area southwest of Jamaica (Caldwell 1966). Juveniles of this species have been taken from several inshore areas in Jamaica as well.

Along the continental margin it has been frequently captured on muddy bottoms from Belize and Nicaragua south to southern Brazil and Uruguay (ca. 37°S). In the northern part of its range along Central America, it has been collected as far north as Belize (17°12′N), but thus far is unknown from the Yucatan Peninsula or Campeche Bay. The absence of this species in the Yucatan region may be explained by upwelling (Rivas 1968) or by changes in the sediments of this region. The Yucatan Shelf is a broad limestone plateau with a minimum of land-derived detrital sediments (Harding 1964, Topp and Hoff 1972). Instead of soft silt and mud sediments typical of more southern locations, sediments on the inner shelf off the Yucatan Peninsula are firmer, consisting of skeletal remains of various planktonic and benthonic organisms, ooids, calcareous pellets, lithic fragments, and grapestone aggregates. This dramatic change from soft, mud substrates to firmer sediments in the Yucatan region may account for the absence of *S. tessellatus* in the waters off southern Mexico.

*Symphurus tessellatus* is one of the most abundant and frequently collected tonguefish species, especially in trawls, from Belize and Honduras south to Venezuela and along the entire coastline of northern South America from the Guianas to about southern Brazil (Meek and Hildebrand 1928, Cervigon 1966, Palacio 1974, Carvalho et al. 1968, Menezes and Benvegnú 1976). Menezes and Benvegnú (1976) described *S. tessellatus* as the most abundant tonguefish collected along the Brazilian coast from about 26°49′S to 4°S in northern Brazil. South of 28°S, it appears to be much rarer, and all specimens I examined from Rio Grande do Sul and south are juveniles. The small size of these specimens suggests that adult *S. tessellatus* may not be regular components of the ichthyofauna of Uruguay and northern Argentina, but that juvenile *S. tessellatus* either seasonally migrate, or are expatriated by passive transport, into waters along the continental shelf and coastline of Uruguay and northern Argentina. Thus it appears that the region south of Rio Grande do Sul, which comes under periodic influence from the cold Falkland Current, does not harbor large populations of this essentially tropical species so common in warmer waters further north.

The specimen from the inner continental shelf of Argentina described by Lazzaro (1973) as *S. plagiusa* and cited in the distribution section for *S. plagusia* (= *S. tessellatus* in the present study) by Menezes and Benvegnú (1976) is probably not a specimen of *S. tessellatus*. Based on the counts and figure provided by Lazzaro, it more closely matches meristic features and has the general body shape of *S. trewavasae*.

**Bathymetric distribution** Throughout its range, juvenile *S. tessellatus* are commonly taken by beach seine in nearshore habitats, and larger adults are frequently captured by trawl in deeper waters. Individuals have been collected from a depth range of 1–86 m (Table 11). There is an ontogenetic migration offshore. Juveniles occur commonly in medium- to high-salinity regions of estuaries and in high-salinity, soft-bottom habitats in nearshore mudflats. Adults generally range into deeper water, although a few large fishes I examined were taken in relatively shallow water. Most of the 349 *S. tessellatus* examined in this study were collected between 1 and 70 m (Table 11), but the majority of captures, and the center of abundance for this species, occurs in depths of 1–50 m (81% of the individuals in this study). The deepest captures are for a single specimen taken at 86 m and 21 individuals at 73 m. The majority of shallow-water captures were specimens smaller than 130 mm SL.

Interestingly, Menezes and Benvegnú (1976) reported that in southern Brazil, *S. tessellatus* (misidentified as *S. plagusia*) occurs only in shallow water (<12 m), though it is known to occur deeper in northern Brazil. They suggested that the presence of *S. jenynsi* off southern Brazil, which generally occurs on the continental shelf at depths greater than 12 m, somehow prevented the occurrence of *S. tessellatus* at these depths. Another explanation is that *S. tessellatus* is primarily a tropical species reaching its southern limit of distribution in southern Brazil south of Rio de Janeiro. Its bathymetric distribution in these waters may be limited not by competitive interaction from *S. jenynsi*; rather, the offshore distribution of *S. tessellatus* may be restricted by cooler water temperatures on the shelf. The appearance of *S. jenynsi*, a temperate-water species (Menezes and Benvegnú 1976), in these regions indicates that temperature may strongly influence the offshore distribution of *S. tessellatus* in southern Brazil.

Throughout its range to at least Rio de Janeiro, juvenile *S. tessellatus* occur in similar habitats and are often collected with a complete size range of *S. plagusia*. In the Caribbean, juvenile *S. tessellatus* are also taken with a complete size range of *S. caribbeanus*. Along the northeastern coast of South America from Surinam to eastern Brazil, large adults of this species are collected in deeper areas with a wide size range of specimens of *S. oculellus* and *S. diomedeanus*.

**Remarks** Comments regarding the nomenclatorial history of this species were reviewed under the "Remarks" section in the account of *S. plagusia*. All authors since Kaup (1858) have considered *S. tessellatus* and *S. plagusia* as conspecific. However, results of this study indicate that *S. plagusia* and *S. tessellatus* are both valid species.

The original description of *Plagusia tessellata* by Quoy and Gaimard (1824) provides sufficient information to clearly identify their specimen. This is the earliest name applied to a tonguefish collected from the southern Brazil region and, therefore, has priority over *Plagusia brasiliensis* Agassiz, in Spix and Agassiz 1831. *Plagusia brasiliensis* was collected at "Bahia," Brazil. The type specimen was thought to have been destroyed during the Second World War (Whitehead and Myers 1971). However, in two recent publications concerning authorship and existence of type specimens described in Spix and Agassiz's "Brazilian Fishes" (1829–31), Kottelat (1984) listed a specimen (MHNN 691) first as the holotype, and later (Kottelat 1988) as a possible syntype of *P. brasiliensis*, thus indicating the existence of at least one specimen from the original account of this nominal species. My examination of this specimen reveals that meristic features lie completely within the range of counts typical for *S. tessellatus* (ID pattern 1-4-3, caudal fin rays 12, dorsal fin rays 99, anal fin rays 83, total vertebrae 53, longitudinal scales 90,

scale rows on head 21, transverse scale count 42). Additionally, the specimen has small ctenoid scales on the blind sides of the dorsal and anal fin rays and a relatively large eye (10.6% HL), features characteristic of *S. tessellatus*. *Plagusia brasiliensis* is therefore regarded as a junior subjective synonym of *Symphurus tessellatus* (Quoy and Gaimard 1824).

In their revision of the tonguefishes occurring in the western South Atlantic, Menezes and Benvegnú (1976) reported that the species they identified as *S. plagusia* had high counts and that the pigmentation consisted of sharply contrasting crossbands with dorsal and anal fins becoming almost black in their posterior portions. These authors found little variation in their material and believed that only a single species was present on the inner continental shelf of southern South America. Menezes and Benvegnú (1976) used the oldest available name, *Symphurus plagusia* (Schneider, in Bloch and Schneider 1801), for their species. These authors also suggested that the subspecific designation for *S. plagusia*, as proposed by Ginsburg (1951), should be reexamined. Based on the high counts and color description of their specimens (strongly banded with fins becoming black posteriorly) and the capture location (open-shelf region where *S. plagusia* [*sensu strictu*] is rare), it is probable that Menezes and Benvegnú had studied only *S. tessellatus*.

**Comparisons** *Symphurus tessellatus* most closely resembles and is completely sympatric throughout the Caribbean and warmer waters of the western South Atlantic with *S. oculellus*, *S. caribbeanus*, and *S. plagusia*. *Symphurus tessellatus* differs from *S. oculellus* in having 4–8 small but well-developed scales on the blind sides of the dorsal and anal fin rays (especially evident in specimens >70 mm SL), a larger eye (79–114, $\bar{x}$ 95 HL in *S. tessellatus* vs. 68–104, $\bar{x}$ 84 HL), and lower meristic values (dorsal fin rays 91–102 vs. 99–106 in *S. oculellus*; anal fin rays 77–86 vs. 81–88; total vertebrae usually 50–53 versus 53–54). *Symphurus tessellatus* lacks a fleshy ridge on the ocular-side lower jaw that is usually present and well developed in *S. oculellus* (compare Figures 4c and 4d). Also, the posterior extension of the jaws is slightly less extensive in *S. tessellatus*, reaching only to about the vertical line through the rear margin of the pupil or rear margin of the lower eye. In *S. oculellus*, the jaws extend further backwards reaching a vertical line through the posterior margin of the eye, and in many specimens the jaws extend slightly posterior to the vertical line through the posterior margin of the lower eye.

*Symphurus tessellatus* generally has about nine wide, dark-brown crossbands; *S. oculellus* has 10–14 (usually 10–12) narrower crossbands. In *S. tessellatus* the caudal fin and the posterior one-third of the dorsal and anal fins are usually dark-brown or black and without an alternating series of blotches and unpigmented areas. In *S. oculellus*, the dorsal and anal fins are not uniformly dark-brown or black; instead, in the posterior two-thirds of the dorsal and anal fins there is an alternating series of blotches and unpigmented areas.

*Symphurus tessellatus*, especially juveniles and small adults (to ~150 mm SL), are superficially similar in overall body shape, relative eye size, and body pigmentation (crossbanding) to *S. caribbeanus*. However, *S. tessellatus* is easily distinguished from *S. caribbeanus* by the black spot on the outer surface of the ocular-side opercle and presence of scales on the blind sides of the dorsal and anal fin rays (both absent in *S. caribbeanus*), and *S. tessellatus* has the posterior dorsal and anal fins, as well as the caudal fin, uniformly darkly-pigmented without alternating blotches and unpigmented areas, and often has black pigment patches on the blind side of the body. In contrast, in *S. caribbeanus*, posterior regions of the vertical fins have alternating dark blotches and unpigmented areas without a progressive darkening in coloration posteriorly in these fins, and the blind side of the body lacks black pigment patches. *Symphurus tessellatus* also has modally higher counts than *S. caribbeanus* (total vertebrae 50–53 vs. 49–50 in *S. caribbeanus*; dorsal fin rays 91–102 vs. 89–96; anal fin rays 77–86 vs. 74–80; 81–96 scales in a longitudinal series vs. 78–89).

*Symphurus tessellatus* can readily be distinguished from *S. plagusia* and *S. civitatium*, and differences between these species were discussed in the "Comparisons" sections under the accounts for *S. plagusia* and *S. civitatium*, respectively.

*Symphurus tessellatus* is quite distinct from other Atlantic tonguefishes. Some meristic values of this species overlap those of *S. marginatus* (Goode and Bean) and *S. diomedeanus*, a species sometimes collected with *S. tessellatus*. Additionally, in the southern extent of its range *S. tessellatus* sometimes co-occurs with *S. jenynsi*.

Although *S. tessellatus* and *S. marginatus* have nearly complete overlap in fin-ray and vertebral counts, such similarities are the only ones between these otherwise distinctive species. Important differences between these species occur in ID pattern (1-4-3 vs. 1-3-2 in *S. marginatus*), hypural number (4 vs. 5), presence of scales on the blind sides of the dorsal and anal fin rays in *S. tessellatus* (absent in *S. marginatus*), and pigmentation features including an unpigmented peritoneum (black in *S. marginatus*), crossbanding on the body, and a black spot on the ocular-side opercle (vs. no crossbanding on body; instead, body with a dark blotch in the caudal region and no opercular spot in *S. marginatus*).

Despite co-occurrence and some morphological similarities, *S. tessellatus* is readily distinguished from *S. diomedeanus* and *S. jenynsi* in caudal-fin-ray number (12 in *S. tessellatus* vs. 10 in the others), and presence of scales on the blind sides of the dorsal and anal fin rays and presence of a black spot on the ocular-side opercle (absent in the others). *Symphurus tessellatus* differs further in lacking a pupillary operculum and the large pigmented spots in the dorsal and anal fins characteristic of *S. diomedeanus*. From *S. jenynsi*, *S. tessellatus* is further distinguished by its much lower meristic values, including 91–102 dorsal fin rays (vs. 107–115), 77–86 anal fin rays (vs. 91–99), and 49–54 total vertebrae (vs. 57–60 in *S. jenynsi*).

There are nine eastern Pacific *Symphurus* with somewhat similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in *S. tessellatus*. Of these nine, only *S. chabanaudi* Mahadeva and Munroe and *S. elongatus* (Günther) are similar to *S. tessellatus* in that they lack a pupillary operculum. Of all species in the genus, *S. tessellatus* is most similar in form, size, and pigmentation pattern to *S. chabanaudi*. However, *S. tessellatus* is distinguished from *S. chabanaudi* primarily by modal differences in the number of dorsal (91–102 vs. 98–109 in *S. chabanaudi*) and anal fin rays (74–86 vs. 82–92); total vertebrae (48–54, usually 50–53 vs. 52–57, usually 53–56); and scales in a longitudinal series (81–96 vs. 92–102 in *S. chabanaudi*). The two species also differ in relative frequencies of occurrence of particular ID patterns. In *S. chabanaudi*, 50% (49/95) of the individuals had a 1-5-3 ID pattern while only 30% (28 specimens) featured a 1-4-3 pattern. In contrast, 173 of 233 (74%) *S. tessellatus* possessed a 1-4-3 ID pattern, while only 6% (13 specimens) had a 1-5-3 pattern.

There is some overlap in fin-ray and vertebral counts between *S. tessellatus* and *S. elongatus*; however, these overlaps are the only similarities between these otherwise distinctive species. *Symphurus tessellatus* has a pattern of crossbands on the body and a large black blotch on the ocular-side opercle, whereas in *S. elongatus* the body is uniformly pigmented without crossbands and this species lacks the prominent black blotch on the ocular-side opercle. Further differences include the presence of small ctenoid scales on blind sides of the dorsal and anal fin rays in *S. tessellatus* (absent in *S. elongatus*) and absence of a fleshy ridge on the ocular-side lower jaw in *S. tessellatus* (a well-developed ridge present in *S. elongatus*). *Symphurus tessellatus* also has a much larger eye (15–21 SL) compared with that of *S. elongatus* (9–15 SL).

The remaining seven eastern Pacific species with meristics comparable to those observed in *S. tessellatus* include *S. fasciolaris*, *S. leei*, *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. melasmatotheca*, and *S. undecimplerus* Munroe and Nizinski. As mentioned above, all of these species, in contrast to *S. tessellatus*, possess a pupillary operculum, and none have the black spot on the ocular-side opercle characteristic of *S. tessellatus*. *Symphurus tessellatus* differs further in caudal-fin-ray number (12) from *S. fasciolaris* (10) and *S. melasmatotheca* and *S. undecimplerus* (each with 11 caudal fin rays). *Symphurus tessellatus* is distinguished from *S. melanurus* in lacking a fleshy ridge on the ocular-side lower jaw (present in *S. melanurus*), in having small ctenoid scales on the blind sides of the dorsal and anal fin rays (usually none or occasionally 1–3 small scales at bases of fin rays in *S. melanurus*), and in having the first dorsal fin ray placed posterior to a vertical through the front margin of the upper eye (versus first dorsal fin ray placed anteriorly to a vertical through front margin of upper eye in *S. melanurus*). *Symphurus tessellatus* is further distinguished from *S. williamsi* in having crossbanding on the body with the posterior portions of the dorsal and anal fins considerably darker than the anterior portions (versus uniform body color without prominent crossbanding and no posterior darkening of dorsal and anal fins in *S. williamsi*). *Symphurus tessellatus* differs from *S. leei* in having an unpigmented peritoneum (versus black in *S. leei*), and the length of the head is smaller than the body depth in *S. tessellatus* (nearly equal to body depth in *S. leei*). *Symphurus tessellatus* is further distinguished from *S. atricaudus* in that it lacks the small ctenoid scales on the ocular-side dorsal and anal fin rays characteristic of that species.

**Material examined** 454 specimens (13.4–220 mm SL).

**Counted and measured** (23 specimens, 96.6–203 mm SL). **Puerto Rico**: UPRM 2717; (142); Puerto Rico; 8 m; 14 Mar 1966. UPRM 2760; (142); Mayaguez; 12 m; 15 Mar 1966. UPRM 2859; (111); Mayaguez; 9 m; 29 Apr 1966. UPRM 3758; (130); Anasco River; 1–2 Jul 1953. UPRM 3759; 2 (130–133); Mayaguez Bay; 1966. **French Guiana**: UF 35275; (172); 5°14′N, 52°06′W; 45 m; 11 Dec 1977. **Brazil**: UFPB 143; 5(96.6–135); Rio Paraiba do Norte; 27 Apr 1978. MHNN 691; (140.3); Bahia (possible holotype or syntype of *Plagusia brasiliensis*). ANSP 121549; 10(108–203); Rio de Janeiro; Jul–Aug 1963.

**Counted** (234 specimens, 64 lots). **Puerto Rico**: MCZ 28843; (91.8); Puerto Rico; 1898–99. UF 83996; (146); beach at Mani, just N of Mayaguez; 16 Apr 1964. UPRM 1590; 2(159–173); Mayaguez; 3 Mar 1962. UPRM 2743; 15(114–172); Mayaguez; 6 m; 15 Mar 1966. UPRM 3760; 2(128–143); Rio Anasco; 17 Aug 1951. UPRM 3761; 3(126–158); Mayaguez Bay; 1966. USNM 126448; (132); Mayaguez; 1899. **Cuba**: MCZ 11269; (111); Cuba. USNM 35108; (81.3); Havana. USNM 37750; (68.6); Havana. USNM 154857; (131); Cuba. **Dominican Republic**: USNM 108369; (123). USNM 108372; (126). **Haiti**: ANSP 81861; (97.7); Port-au-Prince; Nov 1949. ANSP 83626; 8(83.3–113); Port-au-Prince; 1949. ANSP 97661; 6(114–146); Port-au-Prince; 1936. UMMZ 142422; (127); Haiti; 15 Apr 1983. USNM 133671; 3(109–124); Port-au-Prince; 1–4 Jan 1947. USNM 164849; 2(87.7–133); Haiti; 1927. **Jamaica**: LACM 6215; (142); 17°52′N, 77°53′W; 40 m; 15 May 1962. LACM 6217; 10(123–

152); 17°46′N, 77°30′W; 16 m; 15 May 1962. UMML 4831; (115); Hunts Bay; 3 Aug 1958. UMML 34367; 3(118–160); 17°45′N, 77°38′W; 35 m; 15 May 1962. UMML 34368; (144); 17°55′N, 77°51′W; 39 m; 18 May 1965. USNM 37348; (79.9); Jamaica. USNM 291333; 6(128–161); 17°55′N, 77°51′W; 40 m; 18 May 1965. USNM 291347; 2(130–146); 17°53′N, 77°50′W; 42 m; 18 May 1965. USNM 291346; 2(128–138); 17°51′N, 77°49.5′W; 49 m; 18 May 1965. **Belize**: UMML 34354; 4(132–160); 17°12′N, 88°11.2′W; 19 m; 9 May 1967. UMML 34355; 9(134–160); 17°12′N, 88°11.2′W; 19 m; 18 May 1967. **Honduras**: FMNH 100384; 5(38.1–56.0); Brus Lagoon; 10 May 1975. FMNH 94819; 5(37.7–49.5); Brus Lagoon; 10 May 1975. UMML 34348; 2(130–134); 15°49.15′N, 83°44′W; 31 m; 7 Apr 1967. UMML 34349; 2(126–141); 15°48′N, 83°54′W; 24 m; 7 Apr 1967. UMML 34350; 5(111–164); 15°49.5′N, 83°44′W; 31 m; 7 Apr 1967. UMML 34351; 3(130–148); 15°54′N, 83°40′W; 37 m; 8 Apr 1967. UMML 34352; 3(132–155); 15°54′N, 83°40′W; 37 m; 8 Apr 1967. UMML 34353; 2(138–147); 15°45′N, 83°32′W; 35 m; 9 Apr 1967. **Panama**: GCRL 12698; 2(13.4–65.8); Canal Zone; 5 Mar 1974. FMNH 18251-57; 7(50.3–73.3); Panama. **Colombia**: UMML 34369; 4(145–155); 10°53′N, 75°22′W; 42 m; 23 May 1964. UMML 34356; (148); 9°30′N, 76°07.5′W; 41 m; 26 May 1964. USNM 291332; (147); 8°59′N, 76°27′W; 26 m; 29 Nov 1968. **Venezuela**: ANSP 121394; 7(67.9–152); Venezuela; 15 Mar 1962. FMNH 88650; 16(155–200); 12°19′N, 70°34′W; 73 m; 27 Sep 1963. UMML 34370; (173); 11° 52′N, 70°22′W; 35 m; 27 Jun 1968. UMML 34357; (171); 12°19′N, 70°34′W; 73 m; 27 Sep 1963. UMML 34358; (145); 10°29′N, 62° 30′W; 9 m; 24 Oct 1963. **Trinidad**: UPRM 3762; (142); Trinidad; 4 May 1964. **Guyana**: FMNH 86364; (162); 8°09′N, 58°23′W; 42 m; 29 Aug 1958. FMNH 90546; 23(152–204); 8°32′N, 59°10′W; 43 m; 28 Oct 1958. GCRL 3835; (196); 8°13′N, 58°40′W; 37 m; 27 Apr 1969. GCRL 3838; 3(192–202); 9°14′N, 60°19′W; 44 m; 25 Apr 1969. **Surinam**: FMNH 86459; (161); Surinam; *Coquette* 1957. GCRL 23512; 6(164–196); 6°56′N, 54°05′W; 59 m; 2 May 1969. USNM 291335; (168); 6°12′N, 53°23′W; 46 m; 1 Jul 1972. **Brazil**: FMNH 90544; 3(183–196); 1°57′N, 48°12′W; 55 m; 14 Nov 1957. FMNH 91129; (197); 2°29′N, 48°54′W; 86 m; 15 Nov 1957. MCZ 11381; 14(93.9–202); Rio de Janeiro; 1865. MCZ 24939; (174); Rio de Janeiro; 1865. UFPB 1120; 5(51.5–115); Rio Paraíba do Norte; 30 Aug 1981. UFPB uncat.; 9(55.7–123); Rio Paraiba do Norte; 13 Nov 1981. UFPB uncat.; 2(100–110); Rio Paraiba do Norte; 30 Jul 1981. USNM 159225; 2(182–187); 1°57′N, 48°12′W; 55 m; 17 Nov 1957.

**Other material examined** (197 specimens, 70 lots). **Cuba**: MCZ 91961; (89.9); Cuba. **Honduras**: UF 33892; 4(138–154); 15°45′N, 83°32′W; 35 m; 9 Apr 1967. USNM 291345; 6(136–161); 15°56′N, 83°55′W; 47 m; 2 Feb 1967. **Nicaragua**: UMML 34359; 2(126–140); 11°51′N, 83°35′W; 20 m; 28 Jan 1971. UMML 34360; 9(56.4–142); 12°16′N, 83°31′W; 12 m; 28 Jan 1971. **Panama**: GCRL 14930; 2(173–177); Colon; Apr 1974. MCZ 58656; (31.1); Panama; 9 Sep 1964. UF 75622; (57.5); Canal Zone; 1974. UF 76003; (62.8); Canal Zone; Aug 1974. UMML 26664; 2(123–141); 9°18.2–18.4′N, 80°03.3–04′W; 24 m; 20 Jul 1966. USNM 81652; (89.4); Porto Bello; 24–28 Apr 1911. USNM 81653; 2(61.1–67.6); Fox Bay; 11 Jan 1911. USNM 81655; 2(38.1–43.5); Fox Bay; 27 Jan 1912. USNM 144792; (65.1); Canal Zone; 4 Mar 1937. USNM 291351; 3(170–208); 8°25′N, 79°56′W; 10 m; 19 Dec 1963. USNM 291354; 5(189–220); 8°25′N, 79°56′W; 10 m; 19 Dec 1963. **Colombia**: UMML 22247; 22(84–148); 8°48–46.8′N, 76°39.7–42.8′W; 20 m; 12 Jul 1966. UMML 31320; (133); 8°51.9–53.9′N, 76°37.2′W; 12 Jul 1966. USNM 291350; (152); 8°50′N, 76°48′W; 49 m; 2 Nov 1970. USNM 291353; (194); 6°46′N, 54°27′W; 49 m; 28 Jun 1972. USNM 291356; 9(191–207); 6°54′N, 53°58′W; 64 m; 30 Jun 1972. USNM 291352; 3(162–173); 6°34′N, 54°28′W; 37 m; 28 Jun 1972. **Venezuela**: ANSP 120209; (133); Venezuela; 23 Jul 1960–17 Mar 1962. GCRL 3837; (163); 8°52′N, 59°58′W; 29 m; 26 Apr 1969. MCZ 41081; (104); 10°17′N, 69°45′W; 1958. UMML 30197; 30(84–183); 11°25.1–25.8′N, 70°52.1–50′W; 18 m; 27 Jul 1968. UMML 30223; (160); 11°55–55.3′ N, 70°59.9′–71°00′W; 11 m; 28 Jul 1968. UMML 34361; 2(138–185); 10°49′N, 63°13′W; 48 m; 19 Jul 1968. UMML 34362; (187); 10°36′N, 68°12′W; 24 m; 25 Jul 1968. UMML 34363; 6(158–201); 10°11′N, 64°48′W; 35 m; 19 Oct 1963. USNM 291355; 10(144–197); 12°17′N, 70°34′W; 73 m; 27 Sep 1963. USNM 291348; 4(161–185); 11°50′N, 70°40′W; 59 m; 10 May 1965. **Trinidad**: USNM 113251; (124); 10°37′N, 61°42′W; 60 m; 3 Feb 1884. USNM 123112; (179); Gulf of Paria. **French Guiana**: UF 44365; (168); 5°05′N, 51°58′W; 45 m; 11 Dec 1977. **Surinam**: UMML 12251; (162); 6°18′N, 55°11′W; 18 m; 20 Feb 1963. USNM 159536; (177); 6°41′N, 54°17′W; 46 m; 14 Jun 1957. USNM 159567; (205); 6°42′N, 54°12.5′W; 44 m; 14 Jun 1951. USNM 159612; (204); 6°41.5′N, 54°14.5′W; 44 m; 14 Jun 1957. USNM 159618; (194); 6°42.5′N, 54°10′W; 42 m; 14 Jun 1957. USNM 291349; (82.3); 5°30′N, 52°10′W; 51 m; 12 Sep 1958. USNM 291358; 5(126–142); 9°33′N, 76°02′W; 49 m; 28 Nov 1968. **Brazil**: USNM 159237; 6(165–191); 2°00′N, 48°19′W; 46 m; 16 Nov 1957. FMNH 88193; (160); Bahia; 13 Apr 1908. MCP 1198; (116); Florianopolis; 30 Oct 1968. MCP 1199; (114); Florianopolis; 30 Oct 1968. MCP 1200; (118); Florianopolis; 30 Oct 1968. MCP 1202; (116); Florianopolis; 30 Oct 1968. MCP 2193; (156); Florianopolis; Oct 1968. MCP 2194; (112); Florianopolis; Oct 1968. MCP 3139; (126); Florianopolis; Oct 1968. MCP 5663; (180); Port Belo, Santa Catarina. MCP 7270; (128); Port Belo, Santa Catarina; 3–4 Nov 1973. MCP 7327; (126); Porto Belo, Santa Catarina; 1 Aug 1973. MCP 7345; (130); Porto Belo, Santa Catarina; 31 Jul–1 Aug 1973. MCZ 889; 2(123–139); Rio de Janeiro. MCZ 11149; (160); Rio de Janeiro. MCZ 11323; (105); Pernambuco. MCZ 11378; 3(68.7–96.1); Pernambuco. MCZ 11379; (147); Santos. MCZ 11380; (91.7); Curuca. MCZ 11382; (137); Rio de Janeiro. UF 19938; 3(109–133); Sao Paulo; 13 Jul 1961. UFPB 882; 5(36.0–115); Cabedelo; 29 Oct 1981. UFPB uncat.; 5(57.8–107); Ilha da Restinga, Rio Paraiba do Norte. UMML 13292; (186); 4°38′N, 51°05′W; 59 m; 26 Feb 1963. UMML 13977; (157); 2°10′S, 42°24′W; 48 m; 11 Mar 1963. USNM 83172; (94.4); Rio de Janeiro. **Uruguay**: USNM 87772; (119); Montevideo. USNM 87773; (113); Montevideo.

## *Symphurus oculellus*, new species
## Figures 2, 4d, 5, 6b–c

### Synonymy

*Symphurus atricaudus* (not of Jordan and Gilbert 1880). Puyo 1949:179 (French Guyana; counts, color description, poor figure; distinguished from *S. plagusia*).

**Diagnosis** A *Symphurus* characterized by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays; prominent fleshy ridge on ocular-side lower jaw; no pupillary operculum; 99–106 dorsal fin rays; 81–88, usually 83–88, anal fin rays; 52–55, usually 53–54, total vertebrae; 85–98, usually 86–93, scales in longitudinal series; relatively long jaws with posterior extension of maxilla usually reaching to the vertical through posterior margin of pupil of lower eye, occasionally extending to or slightly beyond the vertical through posterior margin of lower eye; relatively small eye (68–104 HL, $\bar{x}$ 84); dorsal fin origin usually at or occasionally slightly anterior to the vertical line through the anterior margin of upper eye; ocular surface dark- to light-brown with 10–14 well-developed, sharply contrasting, somewhat narrow, dark-brown crossbands on head and trunk; outer surface of ocular-side opercle with dark melanophores in diffuse circular pattern or with melanophores coalesced into somewhat rounded pigment spot; inner lining of opercle and isthmus more heavily pigmented on ocular surface than blind side; and dorsal, anal, and caudal fins with an alternating series of pigmented blotches and unpigmented areas.

**Table 16**
Summary of morphometrics expressed in thousandths of standard length (except SL in mm) for the holotype (USNM 159606) and 13 paratypes of *Symphurus oculellus*. (Abbreviations defined in Methods section.)

| | Holotype | Paratypes | | | |
|---|---|---|---|---|---|
| Character | (USNM 159606) | *N* | Range | Mean | SD |
| SL | 144.1 | 14 | 75.8–164 | 142.5 | 21.09 |
| BD | 271 | 14 | 231–297 | 274.5 | 17.19 |
| PDL | 32 | 13 | 32–47 | 38.6 | 4.13 |
| PAL | 199 | 14 | 189–243 | 205.6 | 13.32 |
| DBL | 968 | 13 | 953–968 | 961.4 | 4.13 |
| ABL | 795 | 14 | 765–837 | 793.7 | 18.74 |
| PL | 53 | 12 | 40–64 | 54.3 | 6.08 |
| PA | 37 | 12 | 20–60 | 41.2 | 12.62 |
| CFL | 90 | 14 | 80–99 | 88.9 | 5.53 |
| HL | 180 | 14 | 168–218 | 182.3 | 11.58 |
| HW | 209 | 14 | 198–281 | 216.8 | 21.37 |
| POL | 126 | 14 | 112–153 | 124.8 | 9.38 |
| SNL | 37 | 14 | 34–46 | 38.0 | 3.21 |
| UJL | 46 | 14 | 37–50 | 43.3 | 3.24 |
| ED | 12 | 14 | 12–19 | 15.4 | 1.95 |
| CD | 50 | 14 | 39–63 | 45.4 | 6.39 |
| UHL | 140 | 14 | 126–151 | 139.4 | 6.81 |
| LHL | 98 | 14 | 79–111 | 92.9 | 8.13 |

**Description** *Symphurus oculellus* is a relatively large tonguefish attaining maximum lengths of approximately 189 mm SL. ID pattern usually 1-4-3 (33/38), infrequently 1-3-4 (2), 1-5-3 (1), 1-4-2 (1), or 1-3-3 (1) (Table 1). Caudal fin rays 12 (49/53 specimens), less frequently 11 (Table 2). Dorsal fin rays 99–106 (Table 3). Anal fin rays 81–88, usually 83–88 (Table 4). Total vertebrae 52–55, usually 53–54 (34/37) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 85–98, usually 86–93 (Table 6). Scale rows on head posterior to lower orbit 19–23, usually 19–20 (Table 7). Transverse scales 36–42, usually 38–40 (Table 8).

Proportional measurements appear in Tables 16 and 17. Body relatively elongate with gradual taper posteriorly; body depth relatively narrow (231–297 SL, $\bar{x}$ 274), and nearly uniform from vertical through anal fin rays 10–15 and extending posteriorly to mid-point of body. Preanal length 189–243 SL, $\bar{x}$ 206; somewhat shorter than body depth. Head relatively short (168–218 SL, $\bar{x}$ 182), shorter than body depth. Head relatively wide (198–281 SL, $\bar{x}$ 217); usually greater than head length (HW/HL 1.1–1.5, $\bar{x}$ 1.2); lower head lobe (79–111 SL, $\bar{x}$ 93) considerably narrower than upper head lobe (126–151 SL, $\bar{x}$ 139). Lower opercular lobe of ocular side (264–341 HL, $\bar{x}$ 292) wider than upper opercular lobe (174–246 HL, $\bar{x}$ 211). Postorbital length 112–153 SL, $\bar{x}$ 125. Snout (Fig. 4d) moderately long (190–227 HL, $\bar{x}$ 209), slightly rounded or truncate, covered with small ctenoid scales. Anterior nostril not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind-side snout and chin regions, but not particularly dense, occasionally extending onto ocular-side snout. Jaws relatively long; upper jaw length 221–258 HL, $\bar{x}$ 238; posterior extension of maxilla usually reaching to vertical through posterior margin of pupil of lower eye, occasionally to or slightly beyond vertical through posterior margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 4d). Chin depth 214–291 HL, $\bar{x}$ 248. Lower eye relatively small (68–104 HL, $\bar{x}$ 84); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually only 1–3 small, ctenoid scales in narrow interorbital space. Interorbital space sometimes equaling half the diameter of the lower eye. Pupillary operculum absent. Length of dorsal fin base 953–968 SL, $\bar{x}$ 961. Dorsal fin origin (Fig. 4d) usually at, or occasionally slightly anterior to, vertical line through an-

**Table 17**
Summary of morphometrics expressed as thousandths of head length (except HW/HL) for the holotype (USNM 159606) and 13 paratypes of *Symphurus oculellus*. (Abbreviations defined in Methods section.)

| | Holotype | Paratypes | | |
|---|---|---|---|---|
| Character | (USNM 159606) | Range | Mean | SD |
| HW/HL | 1.2 | 1.08–1.53 | 1.2 | 0.11 |
| POL | 700 | 651–722 | 683.8 | 20.64 |
| SNL | 204 | 190–227 | 209.0 | 11.67 |
| UJL | 254 | 221–258 | 238.3 | 11.74 |
| ED | 69 | 68–104 | 84.3 | 10.52 |
| CD | 277 | 214–291 | 248.4 | 23.62 |
| OPLL | 308 | 264–341 | 292.3 | 23.77 |
| OPUL | 200 | 174–246 | 210.6 | 20.39 |
| UHL | 777 | 661–814 | 767.4 | 44.73 |
| LHL | 542 | 464–556 | 510.3 | 28.01 |

terior margin of upper eye; predorsal length 32–47 SL, $\bar{x}$ 39. Length of anal fin base 765–837 SL, $\bar{x}$ 794. Scales absent from distal two-thirds of blind-side dorsal and anal fin rays. Occasionally with one or two scales occurring sporadically on some blind-side dorsal and anal fin-ray bases. Pelvic fin relatively short, 40–64 SL, $\bar{x}$ 54; longest pelvic fin ray extending posteriorly to base of first or occasionally second anal fin ray; pelvic to anal fin distance 20–60 SL, $\bar{x}$ 41. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 80–99 SL, $\bar{x}$ 89.

Teeth well developed on blind-side jaws. Dentary on ocular side usually with single, mostly incomplete row of slender teeth; premaxilla on ocular side either lacking teeth altogether, or with very short row of teeth covering no more than one-third of premaxilla anterior to the vertical equal with the anterior nostril.

Scales large, ctenoid on both sides of body.

**Pigmentation** Ocular surface ranging from dark- to light-brown with 10–14 (usually 10–12) well-developed, sharply contrasting, somewhat narrow, dark-brown crossbands on head and trunk. Anteriormost crossband on head immediately posterior to eyes; second band situated short distance (usually only 3–4 scales) posteriorly. Throughout most of their vertical extent, two anteriormost bands separate; several specimens with first two crossbands coalesced on ventral portion of opercle forming wide, somewhat circular spot. Crossbands on head somewhat narrower than those on mid- and posterior portions of body. Number of crossbands on trunk variable, differing in degree of completeness, especially in region between opercular opening to point about two-thirds of trunk length. Some bands on body complete, continuous on dorsal and anal fins as dark-brown blotches. Posteriormost crossband situated short distance from caudal fin base, somewhat expanded and slightly arched. Blind side creamy-white. Peritoneum unpigmented. Membrane on blind-side ovary with diffuse pattern of small melanophores (visible only by dissection).

Outer surface of ocular-side opercle with dark melanophores in diffuse pattern or with melanophores sometimes coalesced into somewhat rounded pigment spot. Inner lining of opercle and isthmus more heavily pigmented on ocular surface; blind-side inner opercle with pigmentation restricted to small band of pepper-dot melanophores along ventral margin. Isthmus on blind side not heavily pigmented, but often with pepper-dot pattern of melanophores. Pigment band well developed on ocular-side upper lip; ocular-side lower lip frequently spotted but without well-defined pigment band.

Dorsal, anal, and caudal fins with alternating series of blotches and unpigmented areas. Dorsal fin scarcely pigmented in anterior one-half of body; with series of alternating blotches and unpigmented areas beginning at approximately body mid-point and continuing to posteriormost extent of fin. Anterior one-fourth of anal fin without blotches; posterior three-fourths with pattern of alternating blotches and unpigmented areas as in dorsal fin. Blotches on dorsal and anal fins 3–5 fin rays wide including adjoining membrane. Both dorsal and anal fins with blotches coalescing in posterior one-sixth of fins and forming continuous pigmentation band on fins. Posterior portions of fins becoming gradually darker; blotches, although still present, much more difficult to discern. Distal two-thirds of caudal fin heavily pigmented; proximal one-third relatively lightly pigmented. Caudal fin of most specimens not uniformly pigmented; small cluster of rays (usually 2–4) more lightly pigmented giving appearance of alternating darkly- and lightly-pigmented areas. Smaller number of specimens with entire caudal fin heavily pigmented without pattern of alternating dark and light pigmentation.

**Size and sexual maturity** Among material examined, there were 39 males, 23 females, and five specimens of unknown sex. No significant differences were found between the sexes in overall size; males ranged from 82.2 to 189 mm SL, females were 75.8–180 mm SL. Based on reproductive stages of females, this species attains sexual maturity at about 110 mm SL (Fig. 2). All females larger than 111 mm SL had elongate ovaries. The smallest female, an immature fish of 75.8 mm SL, had only partially elongate ovaries. The

next smallest female was 111 mm SL and had small developing ova in the gonads. All other females were larger than 130 mm SL, had elongate ovaries, and were considered sexually mature.

**Etymology** From the latin "oculus" (eye), plus "ellus" (little), in reference to the relatively small size of the eye in this species compared with that of *S. tessellatus*.

**Geographic distribution** (Fig. 5) A tropical species with a fairly restricted distribution along the inner continental shelf of northeastern South America from Guyana (57°W) to northeastern Brazil (2°S, 40°W) where the majority of specimens have been collected. All but one specimen (UMML 12265; 2°20'S) were collected north of the Amazon outflow. Since little systematic sampling has been conducted on the inner continental shelf off equatorial Brazil, it is not known whether the new species occurs more frequently in areas immediately south of the outflow from the Amazon River.

**Bathymetric distribution** *Symphurus oculellus* occurs at moderate shelf depths (7–110 m) and does not appear to utilize nearshore habitats or estuarine environments as nursery areas as do *S. plagusia* and *S. tessellatus*. Specimens ranging from 76 to 189 mm SL have been collected in offshore habitats, with most (52/57, or 91%) being collected between 11 and 70 m (Table 10). At these depths, it is occasionally collected with adult *S. tessellatus*; however, size differences between the two species in these collections are quite striking. All *S. tessellatus* collected with *S. oculellus* were large adults (>130 mm SL), while the *S. oculellus* were a mixture of sizes, with juveniles as small as 78 and 82 mm SL.

**Remarks** Not all specimens that are the basis of citations in the synonymies of *S. plagusia* and *S. tessellatus* could be examined, so it is impossible to determine if any specimens of *S. oculellus* were included among material listed in earlier accounts on *Symphurus* from northern South America. It is possible that specimens of *S. oculellus* were included in the study by Lowe-McConnell (1962), since some of the trawl stations in that study were at appropriate depths to capture *S. oculellus*. Lowe-McConnell listed all tonguefish captured as *S. plagusia* but did not include descriptive accounts for the specimens, thus preventing positive identification.

The fish described by Puyo as *S. atricaudus* (Jordan and Gilbert) is clearly *S. oculellus*. *Symphurus oculellus* may be distinguished from the eastern Pacific *S. atricaudus* by the following characters: dorsal fin rays 99–106 vs. 94–101 in *S. atricaudus*; anal fin rays 81–88 vs. 77–84; scales 85–98 vs. 104–115. Additionally, *S. oculellus* lacks a pupillary operculum and scales on the blind-side posterior rays of the dorsal and anal fins (both present in *S. atricaudus*).

**Comparisons** Among Atlantic members of the *S. plagusia* complex, *S. oculellus* most closely resembles and is largely sympatric with *S. tessellatus* and *S. plagusia*. Characteristics distinguishing *S. oculellus* from these species were discussed in the "Comparisons" sections under the accounts for *S. plagusia* and *S. tessellatus*, respectively. *Symphurus oculellus* is most easily distinguished from the two remaining Atlantic species belonging to this complex (*S. civitatium* and *S. caribbeanus*) by differences in counts for dorsal fin rays (99–106 vs. 96 or fewer in *S. caribbeanus* and *S. civitatium*), anal fin rays (81–89 vs. 80 or fewer), and total vertebrae (52–55 versus 51 or fewer in *S. caribbeanus* and *S. civitatium*).

Among other Atlantic *Symphurus*, some meristic values of *S. oculellus* overlap those of three relatively deep-water species: the eastern Atlantic *S. vanmelleae* Chabanaud and *S. ligulatus* Cocco, and the western Atlantic *S. marginatus*. Additionally, *S. oculellus* has pigmented dorsal and anal fins reminiscent of those of the sympatrically occurring *S. diomedeanus*. Comparable fin-ray or vertebral counts are the only similarities between *S. oculellus* and the deep-water species. *Symphurus oculellus* is otherwise distinctive from all three species in ID pattern (1-4-3-2-2 vs. 1-2-2-1-2 in *S. vanmelleae*, 1-2-2-2-2 in *S. ligulatus*, and 1-3-2-2-2 in *S. marginatus*), peritoneal pigmentation (unpigmented versus black in the others), and pigmentation of the dorsal and anal fins (alternating series of blotches and unpigmented areas in *S. oculellus* versus uniformly pigmented fins in the other species). From *S. diomedeanus*, *S. oculellus* differs in caudal-fin-ray count (12 vs. 10 in *S. diomedeanus*), and lacks a pupillary operculum (present in *S. diomedeanus*). In *S. oculellus*, the dorsal and anal fins have an alternating series of somewhat rectangular-shaped, pigmented blotches and unpigmented areas beginning in the mid-body region and continuing posteriorly inclusive of the caudal fin, whereas in *S. diomedeanus* the dorsal and anal fins have fewer, nearly spherical spots only in the posteriormost portions of these fins, and the caudal fin usually lacks pigmented spots completely (only rare specimens have a spot present on the caudal fin).

There are seven eastern Pacific *Symphurus* with similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in *S. oculellus*. Of these seven species, only *S. chabanaudi* and *S. elongatus* are similar to *S. oculellus* in lacking a pupillary operculum. Many meristic features of *S. oculellus* completely overlap those of the eastern Pacific

*S. chabanaudi*. *Symphurus oculellus* differs from *S. chabanaudi*, however, in lacking the 4–8 small but well-developed scales on the blind sides of the dorsal and anal fin rays prominent in *S. chabanaudi* specimens, especially those larger than 60 mm; in having a somewhat smaller eye (1.2–1.9, $\bar{x}$ 1.5 SL in *S. oculellus* vs. 1.7–2.3, $\bar{x}$ 1.9 SL), and *S. oculellus* has a well-developed fleshy ridge on the ocular-side lower jaw (absent in *S. chabanaudi*). The posterior extension of the jaws in *S. oculellus* extends to the vertical line through the posterior margin of the eye, and in many specimens the jaws actually extend slightly beyond the posterior margin of the eyes, whereas in *S. chabanaudi* the posterior extension of the jaws reaches only to a vertical line through the rear margin of the pupil or the rear margin of the lower eye. *Symphurus oculellus* also differs from *S. chabanaudi* in the relative frequencies of specimens possessing 1-5-3 and 1-4-3 ID patterns. *Symphurus chabanaudi* has a much higher frequency of occurrence of the 1-5-3 ID pattern (50% of individuals examined) compared with only 30% with a 1-4-3 pattern. In contrast, 40 of 45 (89%) of the *S. oculellus* examined had a 1-4-3 pattern and only one specimen possessed a 1-5-3 pattern.

*Symphurus chabanaudi* also differs from *S. oculellus* in that this species generally has about nine wide, dark-brown crossbands compared with the more numerous (10–14, usually 10–12), narrower bands in *S. oculellus*. In addition, in *S. oculellus* the posterior two-thirds of the dorsal and anal fins usually have an alternating series of blotches and unpigmented areas, whereas in *S. chabanaudi* the posterior one-third of the dorsal and anal fins, and the caudal fin, are usually uniformly dark-brown or black without alternating blotches and unpigmented areas.

There is almost complete overlap in fin-ray and vertebral counts between those of *S. oculellus* and those of *S. elongatus*; however, these species are otherwise distinct. *Symphurus oculellus* has prominent crossbands on the body and a dark blotch on the ocular-side opercle, whereas in *S. elongatus* the body is uniformly pigmented without crossbands, and a prominent blotch on the ocular-side opercle is wanting.

The remaining five eastern Pacific species with meristics comparable to those observed in *S. oculellus* include *S. leei*, *S. atricaudus*, *S. melanurus*, *S. williamsi*, and *S. undecimplerus*. These species, in contrast to *S. oculellus*, possess a pupillary operculum, and none features the pigmented blotch found on the ocular-side opercle in *S. oculellus*. *Symphurus oculellus* differs further from *S. undecimplerus* in caudal-fin-ray number (12 vs. 11); is distinguished from *S. melanurus* and *S. williamsi* in having the dorsal and anal fins with an alternating series of pigmented blotches and unpigmented areas (versus dorsal and anal fins without an alternating series of pigmented blotches and unpigmented areas in these other species); is readily distinguished from *S. leei* in having an unpigmented peritoneum (versus black in *S. leei*) and in having the head length smaller than body depth (nearly equal to body depth in *S. leei*); and differs from *S. atricaudus* in lacking the small ctenoid scales on the ocular-side dorsal and anal fin rays characteristic of that species.

**Material examined** 69 specimens (75.8–189 mm SL).

**Counted and measured** (14 specimens, 75.8–164 mm SL). **Holotype:** USNM 159606; female, 144 mm SL; Surinam (6°24′N, 55°00′W); 27 m; 11 May 1957. **Paratypes. Guyana:** BMNH 1950.5.15: 51; (139); off Georgetown. FMNH 86365; (148); 7°05′N, 57°12′W; 33 m; 1 Sep 1958. FMNH 88846; (132); 6°54′N, 57°47′W; 18 m; 25 Mar 1963. **Surinam:** USNM 159559; (75.8); 6°04′N, 54°51′W; 70 m; 13 May 1951. ZMA 111.212; (158); 5°15′N, 55°15′W; 12 m; 13 Oct 1969. **French Guiana:** UMML 12254; (141); 6°17′N, 53°35′W; 40 m; 21 Feb 1963. USNM 313518; 2(143–151); 6°12′N, 53°23′W; 46 m; 1 Jul 1972. UMML 11549; (156); 5°57′N, 52°18′W; 70 m; 22 Feb 1963. UMML 12262; (148); 5°24′N, 51°34′W; 64 m; 23 Feb 1963. ZMA 111.234; (140); 3°45′N, 51°45′W; 40 m; 16 Nov 1969. **Brazil:** FMNH 86362; (155); 1°57′N, 48°15′W; 48 m; 17 Nov 1957. FMNH 100385; (164); 1°57′N, 48°12′W; 55 m; 14 Nov 1957.

**Counted** (30 paratypes, 14 lots). **Guyana:** BMNH 1961.9.4:117; (189). BMNH 1961.9.4:118; (163). UMML 34335; (136); 7°42′N, 57°32′W; 27 m; 15 Jul 1968. **Surinam:** GCRL 3836; 5(130–165); 6°56′N, 54°05′W; 2 May 1969. UMML 12249; (143); 6°18′N, 55°11′W; 18 m; 20 Feb 1963. ZMA 111.228; 1; 5°15′N, 55°15′W; 12 m; 10 Oct 1969. FMNH 90552; 2(142–147); Surinam; 18 m; 1957. FMNH 90553; (144); Surinam; 110 m; 3 May 1957. FMNH 91368; (141); Surinam; 1957. **French Guiana:** FMNH 100386; 7(154–180); 6°03′N, 52°22′W; 65 m; 13 Sep 1958. FMNH 90085; 5(163–180); 5°46′N, 52°02′W; 70 m; 12 Nov 1957. FMNH 86397; (130); 5°05′N, 52°14.5′W; 20 m; 23 May 1957. **Brazil:** FMNH 100387; 2(140–155); 2°29′N, 48°54′W; 86 m; 15 Nov 1957. USNM 159541; (150); 2°29′N, 48°55′W; 42 m; 15 Nov 1957.

**Other non-type material examined** (25 specimens, 14 lots). **Guyana:** UMML 34364; (152); 7°00′N, 57°08′W; 26 m; 15 Jul 1968. **Surinam:** UMML 12498; (158); 7°01′N, 54°21′W; 64 m; 21 Feb 1963. FMNH 90223; (135); 6°54′N, 54°47′W; 18 m; 25 Mar 1953. UMML 34334; 2(104–140); 6°25′N, 55°04′W; 7 m; 10 Jul 1968. FMNH 91109; (151); 6°24.5′N, 55°02.5′W; 27 m; 11 May 1957. USNM 159602; 2(82.2–94.8); 6°23′N, 55°05.5′W; 27 m; 11 May 1957. USNM 313515; 3(136–152); 6°21′N, 54°28′W; 28 m; 29 Jun 1972. UMML 12310; 3(139–142); 6°11′N, 55°39′W; 15 m; 19 Feb 1963. **French Guiana:** UMML 13301; 6(111–175); 6°00′N, 52°27′W; 64 m; 22 Feb 1963. UMML 13307; (166); 5°29′N, 51°37′W; 64 m; 23 Feb 1963. UF 83997; (143); 5°05′N, 51°58′W; 45 m; 11 Dec 1977. USNM 313516; (147); 4°47′N, 51°37′W; 33 m; 5 May 1975. UMML 34336; (160); off Cayenne; F. Berry, Station 10, 12. **Brazil:** UMML 12265; (150); 2°20′S, 40°24′W; 40 m; 12 Mar 1963.

## *Symphurus caribbeanus*, new species
## Figures 2, 4e, 5, 6d

### Synonymy

*Symphurus plagusia plagusia.* Ginsburg 1951:220 (in part) (Fox Bay, Panama; specimens in USNM 81654 included in account of *S. p. plagusia*).

*Symphurus plagusia.* Austin and Austin 1971:38 (in part) (Guayanilla, Puerto Rico; food habits; nine specimens from UPRM 2926 belong to the new species).

**Diagnosis** A *Symphurus* with the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal fin rays; unpigmented peritoneum; relatively large eye (82–110 HL); no fleshy ridge on ocular-side lower jaw; without a pupillary operculum; no small ctenoid scales on the blind sides of the dorsal and anal fin rays; dorsal fin rays 89–96, usually 92–96; anal fin rays 74–80; total vertebrae 48–51, usually 49–50; 78–89 scales in longitudinal series; relatively short jaws usually extending to the vertical line through the posterior margin of pupil of lower eye or occasionally extending to the vertical through posterior margin of lower eye; dorsal fin origin usually reaching, or occasionally slightly anterior to, vertical line through front margin of upper eye; ocular surface dark-brown to almost yellow; usually with 10–15 narrow, irregularly complete, sharply contrasting, dark-brown crossbands on head and trunk; outer surface of ocular-side opercle without dark blotch; inner lining of opercle and isthmus heavily pigmented on ocular side, unpigmented on blind side; entire dorsal and anal fins with alternating series of blotches and unpigmented areas.

**Description** A medium-sized tonguefish attaining maximum lengths of approximately 122 mm SL. ID pattern usually 1-4-3 (67/82), less frequently 1-3-3 (8), 1-3-4 (23), or 1-4-4 (2) (Table 1). Caudal fin rays usually 12 (78/82), less frequently 11, 10, or 13 (Table 2). Dorsal fin rays 89–96, usually 92–96 (Table 3). Anal fin rays 74–80 (Table 4). Total vertebrae 48–51, usually 49–50 (75/79) (Table 5); abdominal vertebrae 3+6. Hypurals 4. Longitudinal scale rows 78–89 (Table 6). Scale rows on head posterior to lower orbit 17–22, usually 19–21 (Table 7). Transverse scales 36–44 (Table 8).

Proportional measurements appear in Tables 18 and 19. Body relatively deep (277–320 SL, $\bar{x}$ 301); with greatest depth in anterior one-third of body followed by relatively rapid taper posteriorly. Preanal length 191–261 SL, $\bar{x}$ 223; somewhat shorter than body depth. Head relatively short (185–224 SL, $\bar{x}$ 199); considerably shorter than body depth. Head relatively wide (220–268 SL, $\bar{x}$ 240); greater than head length (HW/HL 1.1–1.3, $\bar{x}$ 1.2); lower head lobe (84–111 SL, $\bar{x}$ 99) considerably narrower than upper head lobe (152–184 SL, $\bar{x}$ 165). Lower opercular lobe of ocular side (241–348 HL, $\bar{x}$ 292) considerably wider than upper opercular lobe (162–277 HL, $\bar{x}$ 199). Postorbital length 119–143 SL, $\bar{x}$ 134. Snout moderately long (193–255 HL, $\bar{x}$ 218) and pointed (Fig. 4e), covered with small ctenoid scales. Anterior nostril usually not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed on blind side of snout and chin regions, but not particularly dense. Jaws relatively short; upper jaw length 195–253 HL, $\bar{x}$ 231; posterior extension of maxilla usually reaching to vertical line through posterior margin of pupil or occasionally posterior margin of lower eye. Ocular-side lower jaw without distinct, fleshy ridge near posterior margin (Fig. 4e). Chin depth 227–305 HL, $\bar{x}$ 260. Lower eye moderately large (82–110 HL, $\bar{x}$ 97); upper eye usually slightly anterior to lower eye; eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Length of dorsal fin base 952–972 SL, $\bar{x}$ 964. Dorsal fin origin (Fig. 4e) usually reaching, or occasionally slightly anterior to, vertical line through front margin of upper eye; predorsal length 29–48 SL, $\bar{x}$ 36. Length of anal fin base 751–820 SL, $\bar{x}$ 781. Scales absent on blind sides of dorsal and anal fin rays. Pelvic fin relatively short, 51–75 SL, $\bar{x}$ 63; longest pelvic fin ray usually reaching base of first or

**Table 18**
Summary of morphometrics expressed in thousandths of standard length (except SL in mm) for the holotype (USNM 313487) and 20 paratypes of *Symphurus caribbeanus*. (Abbreviations defined in Methods section.)

| | Holotype | Paratypes | | |
|---|---|---|---|---|
| Character | (USNM 313487) | Range | Mean | SD |
| SL | 100.5 | 40.1–121.9 | 84.5 | 22.40 |
| BD | 317 | 277–320 | 300.6 | 12.14 |
| PDL | 34 | 29–48 | 36.2 | 5.45 |
| PAL | 219 | 191–261 | 223.0 | 15.89 |
| DBL | 966 | 952–972 | 964.3 | 5.70 |
| ABL | 792 | 751–820 | 781.0 | 18.89 |
| PL | 62 | 51–75 | 63.2 | 6.56 |
| PA | 45 | 35–63 | 47.6 | 6.62 |
| CFL | 106 | 87–116 | 102.4 | 7.56 |
| HL | 194 | 185–224 | 199.2 | 10.94 |
| HW | 239 | 220–268 | 240.0 | 11.03 |
| POL | 123 | 119–143 | 133.6 | 6.72 |
| SNL | 45 | 36–54 | 43.5 | 4.92 |
| UJL | 49 | 37–56 | 46.2 | 4.85 |
| ED | 20 | 17–22 | 19.4 | 1.56 |
| CD | 52 | 43–64 | 51.8 | 5.06 |
| UHL | 141 | 152–184 | 164.6 | 32.23 |
| LHL | 112 | 84–111 | 98.6 | 26.53 |

**Table 19**
Summary of morphometrics expressed as thousandths of head length (except HW/HL) for the holotype (USNM 313487) and 20 paratypes of *Symphurus caribbeanus*. (Abbreviations defined in Methods section.)

| | Holotype | Paratypes | | |
|---|---|---|---|---|
| Character | (USNM 313487) | Range | Mean | SD |
| HW/HL | 1.2 | 1.1–1.3 | 1.2 | 0.06 |
| POL | 636 | 632–744 | 671.6 | 28.72 |
| SNL | 231 | 193–255 | 218.4 | 18.47 |
| UJL | 251 | 195–253 | 231.3 | 15.96 |
| ED | 103 | 82–110 | 97.4 | 7.18 |
| CD | 267 | 227–305 | 259.8 | 19.74 |
| OPLL | 359 | 241–359 | 291.8 | 32.23 |
| OPUL | 236 | 162–274 | 199.4 | 27.34 |
| UHL | 728 | 725–973 | 828.0 | 57.84 |
| LHL | 580 | 437–592 | 495.7 | 39.42 |

occasionally second anal fin ray; pelvic to anal fin distance 35–63 SL, $\bar{x}$ 48. Posteriormost pelvic fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to origin of anal fin base (membrane torn in most specimens). Caudal fin relatively short, 87–116 SL, $\bar{x}$ 102.

Teeth well developed on blind-side jaws. Upper and lower jaws on ocular side usually with small patch of teeth covering only anterior one-third of jaw, or lacking teeth altogether.

Scales moderate in size, strongly ctenoid on both sides of body.

**Pigmentation** Pattern of body pigmentation generally similar for both sexes at all sizes, but mature males with more intense pigmentation on body and posterior portions of dorsal and anal fins. Ocular surface dark-brown to almost yellow; usually with 10–15 narrow, irregularly complete, sharply contrasting, darker-brown crossbands on head and trunk. Crossbands not continued onto dorsal and anal fins. Anteriormost band on head immediately posterior to eyes. Second band crossing head just anterior to opercular opening. Crossbands on trunk variable in number, usually 3–6 scale rows in width. First band crossing body immediately posterior to opercular opening. Posteriormost band slightly anterior to caudal fin base, irregularly complete. Blind side off-white. Peritoneum unpigmented. Outer surface of ocular-side opercle with general background pigmentation. Dorsal margin of ocular-side opercle sometimes with dusky blotch due to dark pigmentation of inner lining of operculum showing through to outer surface. Inner lining of opercle and isthmus heavily pigmented on ocular side; unpigmented on blind side. Slight band of pigment on ocular-side upper lip; ocular-side lower lip frequently spotted but without definite band of pigment.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. Except for anteriormost portion of dorsal fin, entire dorsal and anal fin with alternating series of dark blotches and unpigmented areas. Blotches variable in shape, most frequently nearly rectangular; extending from base almost to distal tip of fin rays; blotches usually covering 2–5 fin rays alternating with 2–4 lightly-pigmented fin rays. Caudal fin either uniformly darkly-pigmented, or with alternating series of pigmented blotches and unpigmented areas throughout length of fin.

**Size and sexual maturity** Adult *S. caribbeanus* range in size from approximately 71 to 122 mm SL, and this species is one of the smallest members of the *S. plagusia* complex. Size-related life-history information is derived from data taken from 89 specimens. Males and females attain similar sizes. The largest fish measured was a gravid female (122 mm SL); largest male was (120 mm SL).

There were 44 males (52.9–122 mm SL), 39 females (55.6–122 mm SL), and 6 immature fish (24.4–43.8 mm SL) among material examined. Based on reproductive stages of females, this species matures at 70–80 mm SL (Fig. 2). There were 30 mature females ranging in size from 71.8 to 122 mm SL. All females larger than 80 mm SL were mature. The smallest mature female (71.8 mm SL) was unusual because six of seven others in this size range had undeveloped gonads.

Of 39 females, nine, ranging from 55.6 to 79.1 mm SL, were immature with only partially elongate ovaries. The smallest immature females (55.6, 56.9 mm SL) had only partially elongate ovaries, whereas some larger immature females (58.1–79.1 mm SL) had more developed ovaries but were without obviously developing ova.

**Etymology** This species is named after its area of occurrence in reference to its common but apparently restricted distribution to habitats within the Caribbean Sea.

**Geographic distribution** (Fig. 5) Widely distributed in the Caribbean Sea. *Symphurus caribbeanus* has been collected along coastal margins of central and northern South America and off islands fringing the Caribbean Sea. Islands where this species has been collected include St. Martin and Cuba, but most specimens examined were taken at Puerto Rico and Haiti. This species has been collected at coastal locations in Nicaragua, Costa Rica, and Panama along

Central America, and also along the Caribbean coast of Colombia.

**Bathymetric distribution** *Symphurus caribbeanus* inhabits shallow water. Of 94 specimens for which depth information was available, the majority (78/94, 83%) were collected in 20 m or less (Table 11), and approximately half were collected in waters shallower than 10 m. All life stages are represented among the shallowest collections. The deepest capture (29 m) is for one lot (UMML 34341) comprising 16 individuals.

**Ecology** Other than depth of occurrence and geographic distribution, little is known about ecological requirements of this species. Austin and Austin (1971) included nine specimens of *S. caribbeanus* in their survey of feeding habits of fishes inhabiting mangrove areas in southwestern Puerto Rico. These specimens, ranging in size from 30 to 104 mm SL, had fed mostly on polychaetes and small, benthic crustaceans, and individuals collected at night had undigested food in their stomachs, suggesting nocturnal feeding.

**Comparisons** Among Atlantic members of the *S. plagusia* complex, *S. caribbeanus* most closely resembles and occurs sympatrically with *S. plagusia* and juvenile and subadult *S. tessellatus*. There is overlap also in some meristic features of *S. caribbeanus* and *S. civitatium*, but these species are otherwise quite distinct. *Symphurus caribbeanus* differs considerably from *S. oculellus*. Differences between *S. caribbeanus* and these other species were discussed previously in "Comparisons" sections under the accounts for *S. plagusia*, *S. civitatium*, *S. tessellatus*, and *S. oculellus*.

Meristic values of *S. caribbeanus* overlap those of 11 other Atlantic species of *Symphurus*. *Symphurus caribbeanus* is readily distinguished from six deep-water Atlantic species with similar meristic values (*S. marginatus* (Goode and Bean) and *S. piger*, occurring in the Gulf of Mexico and Caribbean; two western North Atlantic species, *S. pusillus* and undescribed species C of Munroe (1987); the western South Atlantic *S. ginsburgi* Menezes and Benvegnú; and the eastern Atlantic *S. nigrescens*) in ID pattern (1-4-3 vs. 1-3-2 in the others) and peritoneal pigmentation (unpigmented versus dark-black, visible through both sides of abdominal wall in the others). *Symphurus caribbeanus* differs from two diminutive eastern Atlantic species, *S. lubbocki* and *S. reticulatus*, in ID pattern (1-4-3 vs. 1-3-2), dentition on ocular-side jaws (absent or reduced in *S. caribbeanus* versus complete row in the others), and longitudinal scale counts (78–89 in *S. caribbeanus* versus 95 or more in *S. lubbocki* and *S. reticulatus*). *Symphurus caribbeanus* differs from the eastern Atlantic *S. normani* in ID pattern (1-4-3 vs. 1-3-3), peritoneal pigmentation (unpigmented versus spotted in *S. normani*), and *S. caribbeanus* lacks the small ctenoid scales on the blind sides of the dorsal and anal fin rays that are present in *S. normani*. *Symphurus caribbeanus* differs further from the western South Atlantic *S. trewavasae* and *S. kyaropterygium* Menezes and Benvegnú, in caudal-fin-ray count (12 vs. 10) and ID pattern (1-4-3 vs. 1-3-3 in *S. trewavasae*, 1-4-2 in *S. kyaropterygium*). *Symphurus caribbeanus* also lacks the pupillary operculum and fin membrane ostia characteristic of *S. kyaropterygium*.

Three shallow-water, western Atlantic species—*S. diomedeanus*, which occurs in sympatry with *S. caribbeanus*, and the allopatric *S. plagiusa* and *S. urospilus* Ginsburg—have meristic features similar to those of *S. caribbeanus*. *Symphurus caribbeanus* differs from these species in caudal-fin-ray count (12 vs. 10 in *S. diomedeanus* and *S. plagiusa*, 11 in *S. urospilus*) and pigmentation of the vertical fins. The vertical fins of *S. caribbeanus* have an alternating series of blotches and unpigmented areas and the caudal fin lacks an ocellated spot, unlike the vertical fins in *S. diomedeanus* which have fewer, nearly spherical spots; or those of *S. plagiusa* and *S. urospilus*, that are uniformly pigmented without darkly-pigmented blotches throughout their lengths; or the caudal fin in *S. urospilus* that has an ocellated spot. From *S. plagiusa*, *S. caribbeanus* further differs in the absence of a black opercular spot and the small ctenoid scales on the blind-side dorsal and anal fins characteristic of *S. plagiusa*. *Symphurus caribbeanus* is further distinguished from *S. diomedeanus* and *S. urospilus* in lacking a pupillary operculum (present in the others).

Meristic values of *S. caribbeanus* overlap those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern, including *S. leei*, *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. fasciolaris*, and *S. melasmatotheca*. *Symphurus caribbeanus* differs from all of these species in lacking a pupillary operculum (present in the others). Of all these species, *S. caribbeanus* appears most similar to *S. williamsi* but differs in lacking small ctenoid scales on the blind sides of the dorsal and anal fin rays (present in *S. williamsi*) and in having pigmented blotches in the dorsal and anal fins (versus dorsal and anal fins without blotches in *S. williamsi*). *Symphurus caribbeanus* also differs from *S. atricaudus* in lacking small ctenoid scales on the ocular-side dorsal and anal fin rays and in having an alternating series of pigmented blotches in the dorsal and anal fins (scales present and fins uniformly pigmented in *S. atricaudus*). From *S. melanurus*, *S. caribbeanus* differs in that *S. melanurus* possesses a fleshy ridge on the ocular-side lower jaw and the first dorsal fin ray reaches a vertical equal with or anterior to the anterior margin of the upper eye, whereas *S. caribbeanus* lacks a fleshy

ridge on the ocular-side lower jaw and the first dorsal fin ray is usually placed posterior to the vertical through the front margin of the upper eye. These two species are further distinguished by the fewer scales in a longitudinal series (78–89 in *S. caribbeanus* vs. 89–108 in *S. melanurus*), the lightly-pigmented inner lining on the blind-side opercle (versus darkly-pigmented inner lining on the blind-side opercle in *S. melanurus*), and because the posterior dorsal and anal fins and the caudal fin of *S. caribbeanus* have an alternating series of pigmented blotches and unpigmented areas (versus progressive darkening in posterior dorsal and anal fins without alternating series of blotches and unpigmented areas in *S. melanurus*). *Symphurus caribbeanus* differs from *S. fasciolaris* and *S. melasmatotheca* in possessing 12 caudal fin rays (versus 10 and 11 in *S. fasciolaris* and *S. melasmatotheca*, respectively) and in lacking an ocellated spot on the caudal fin (present in *S. fasciolaris*) or pigmented peritoneum (present in *S. melasmatotheca*). From *S. leei*, *S. caribbeanus* is further distinguished in having the head length considerably smaller than the body depth (head length nearly equal with body depth in *S. leei*), in its smaller eye (17–22 SL vs. 22–27 SL in *S. leei*), and in having an unpigmented peritoneum (black in *S. leei*).

**Material examined** 100 specimens (24.4–122mm SL).

**Counted and measured** (21 specimens, 40.1–122mm SL). **Holotype**: USNM 313487; male, 100.5mm SL; Mayaguez Bay, Puerto Rico; 1966; Collected by J.S. Ramsey. **Paratypes. Haiti**: FMNH 61574; (40.7); Port-au-Prince Bay; 12 Sep 1953. **Netherlands Antilles**: UMML 5297; (40.1); St. Martin; 1m; 2 Jul 1959. **Puerto Rico**: UPRM 740; 2(120–122); Río Anasco; 1–2 Jul 1953. UPRM 1588; (98.0); Mayaguez; Mar 1962. UPRM 2926; 8(58.1–97.9); Guayanilla; 23 Jul 1968. ANSP 118553; (69.8); Puerto Rico; 25 Jan 1971. **Colombia**: UMML 30087; 6(88.7–98.1); 8°44.5–45.6′N, 76°52.71′W; 4m; 12 Jul 1966.

**Counted** (2 **paratypes**, 1 lot)—**Colombia**: USNM 313513; 2(102.8–116.7); Bajo-Sabanilla, off Barranquilla; 8 Sep 1969. (60 **non-type specimens**, 10 lots)—**Puerto Rico**: ANSP 115601; 7(43.3–82.5); Puerto Yabucoa; 12–13 Jul 1969. UPRM 736; (95.8); Río Anasco; 17 Aug 1951. UPRM 740; 8(90.0–122); Río Anasco; 1–2 Jul 1953. **Cuba**: MCZ 11200; (71.8); 1851. **Haiti**: UF 83998; 10(80.7–95.4); 2km NW of Port Salut; sandy beach near eelgrass bed; 1m; 7 Apr 1979. UMML 34337; 3(95.8–110). **Nicaragua**: UMML 34338; 2(79.1–94.3); 12°16′N, 83°31′W; 12m; 28 Jan 1971. **Panama**: UMML 34339; (115); 8°49′N, 81°13′W; 18m; 21 Jul 1966. UMML 34340; 26(24.4–117); 9°48′N, 82°50′W; 19m; 26 Jan 1971. USNM 313514; (46.2); Colon; 5 Jan 1911.

**Other non-type material examined** (17 specimens, 2 lots). **Cuba**: MCZ 25982; (108.7). **Costa Rica**: UMML 34341; 16(52.9–117); 10°40′N, 83°29′W; 29m; 27 Jan 1971.

## Comparative life histories and distributions

In addition to morphological and pigmentation differences among Atlantic members of the *S. plagusia* complex, significant differences among members of this species complex are evident in geographic ranges, ecologies (primarily bathymetric occurrence), and life-history traits, including adult sizes and minimal sizes at sexual maturity. With the exception of *S. civitatium*, which occurs allopatrically in coastal seas off the southeastern United States and northern Mexico, these species occur in the Caribbean Sea and South Atlantic Ocean. Two species, *S. plagusia* and *S. tessellatus*, have extensive and sympatric distributions, ranging throughout insular and coastal locations from the northern Caribbean Sea to as far south as Rio de Janeiro, Brazil, for *S. plagusia* and to northern Uruguay for *S. tessellatus*. The geographic ranges of both *S. plagusia* and *S. tessellatus* completely overlap those of *S. caribbeanus* and *S. oculellus*, species with more restricted distributions. *Symphurus caribbeanus* occurs throughout insular and coastal areas in the Caribbean, with its southernmost occurrence in the western Caribbean off Colombia. *Symphurus oculellus* has the most restricted distribution of the species complex, occurring on the continental shelf along the northern coast of tropical South America north of 5°S from approximately 40°–60°W longitude.

Overall, members of the *S. plagusia* complex are generally shallow-water species, inhabiting nearshore and coastal seas usually shallower than 80m (Table 11). Only rarely have individuals been collected deeper than 80m, and none have been taken at depths greater than 110m. In contrast, of the other eleven Atlantic species possessing 12 caudal fin rays (all have a 1-3-2 ID pattern), seven species usually inhabit much deeper waters on the continental shelf and upper continental slope, ranging from 35 to 700m, with centers of abundance usually between 100 and 350 m (Munroe 1987). Exceptional to this observation are four diminutive species (*S. arawak* Robins and Randall, *S. rhytisma* Böhlke, *S. lubbocki*, and *S. reticulatus*), which occur on shallow substrates adjacent to coral reefs.

Although three of the five Atlantic species of the *S. plagusia* complex are known to have overlapping geographic ranges, the species do not occur syntopically at all life-history stages, especially with respect to bathymetric occurrences (Table 11). Three of the five Atlantic members of the *S. plagusia* complex, *S. plagusia*, *S. tessellatus*, and *S. caribbeanus*, occur syntopically at some stage in their life history in shallow waters of the Caribbean. Juveniles of all three species have been taken exclusively in beach seine and otter

trawl collections in shallow-water (<10m) estuarine and mudflat habitats. However, striking differences are apparent in how these species utilize inshore habitats. In these habitats, juvenile *S. tessellatus* are collected with all life history stages of *S. plagusia* and *S. caribbeanus*. Adult *S. tessellatus*, however, apparently undergo an ontogenetic migration from shallow, nearshore habitats to deeper waters further offshore (11–80m) on the continental shelf. In contrast, although a small number of *S. caribbeanus* and *S. plagusia* have been taken as deep as 30–40m on the continental shelf, these were isolated captures of large adults (>110mm SL). The majority of *S. plagusia* and *S. caribbeanus* (80% and 83%, respectively), including all juveniles examined, were collected in waters shallower than 20 m. Most specimens were taken by beach seine and small otter trawls at depths shallower than 10m in nearshore mudflats, mangrove habitats, and estuarine locations.

*Symphurus oculellus*, although occurring sympatrically with *S. plagusia* and *S. tessellatus* (see Figures 3 and 5), apparently has a different life history than these other species. *Symphurus oculellus* inhabits deeper waters than the others (Table 11), spanning an overall bathymetric range of 7–110m, but being captured most frequently in waters deeper than 20m (78% collected deeper than 20m). *Symphurus oculellus*, including juveniles as small as 76mm SL, have been collected in neritic waters deeper than 7m and none have been taken from estuarine habitats, contrary to *S. plagusia* and *S. tessellatus*. However, estuarine environments in the geographic range of *S. oculellus* along northeastern South America have not been as thoroughly sampled as have those nearshore habitats occupied by *S. plagusia* and juvenile *S. tessellatus* in the northern Caribbean and southern Brazilian areas. *Symphurus civitatium*, the northernmost-occurring species, is the only Atlantic species with a distribution allopatric to those of other members of this species group. Adult *S. civitatium* are very abundant in collections and, although inhabiting a wide depth range (1–73m), are more commonly captured between 11 and 45m on the inner continental shelf where approximately 91% (199/216) of the specimens examined in the present study were collected (Table 11). It is unusual for adult *S. civitatium* to occur in habitats deeper or shallower than this depth range. For example, the deepest captures of this species were made at 73 and 62m, where a single fish was taken each time, and of four fish collected in waters shallower than 10m, only one was an adult and three others were small juveniles (<35mm SL). Little is known concerning early-life-history stages of *S. civitatium*. Few juveniles have been collected, but all of these were taken at inshore locations. The occurrence of early-life-history stages in nearshore waters suggests a life-history pattern similar to that of *S. tessellatus*, where adults occur in deeper waters on the inner continental shelf and juveniles inhabit estuarine or nearshore nurseries. However, distribution data for this species, especially for early juveniles, are too incomplete to estimate how regularly this species utilizes inshore waters as nurseries. Further investigation is needed on whether recent captures of early juveniles in estuarine environments represent isolated occurrences of this species or its normal life-history pattern.

Among *Symphurus*, members of the *S. plagusia* complex are medium- to large-sized tonguefishes, ranging in maximum lengths from 122mm SL for *S. caribbeanus* to 220mm SL for *S. tessellatus*, the second largest species of tonguefish in the Atlantic (only *S. jenynsi* from the southern South Atlantic exceeds these sizes) and third largest in the genus (Fig. 2). *Symphurus caribbeanus* and *S. plagusia* are the smallest of the five Atlantic species of this complex (122 and 130mm SL, respectively), and also mature at the smallest sizes (70–80mm SL for *S. caribbeanus*; 80mm SL for *S. plagusia*). *Symphurus civitatium* is only slightly larger, attaining maximum lengths of ~152mm SL and maturing at sizes slightly greater than 90mm SL. *Symphurus oculellus* and *S. tessellatus* are the largest Atlantic species in this complex, attaining maximum sizes of 189 and 220mm SL, respectively. Not surprisingly, these larger-sized species also mature at somewhat larger sizes. Female *S. oculellus* mature at about 110mm SL and female *S. tessellatus* at 104–120mm SL.

Comparisons of ecological and life-history parameters, like those above, supplement and corroborate systematic determinations based on morphological evidence. However, in the absence of a cladistic hypothesis, the value of these ecological comparisons, especially concerning historical relationships, either of the species complex within the genus or of the individual species comprising the *S. plagusia* complex, cannot be fully assessed. Further study, based on shared derived characters using outgroup comparisons or ontogeny, is needed before intrageneric relationships of the species complex and interrelationships of its members can be determined to better understand trends in the evolution of life-history attributes of these tonguefishes.

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# Geographic Variation in Morphometric Characters and Gill-Raker Counts of Yellowfin Tuna *Thunnus albacares* from the Pacific Ocean

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**Abstract.**—Samples of yellowfin tuna *Thunnus albacares* from five different areas of the Pacific Ocean, Mexico, Ecuador, Australia, Japan, and Hawaii, collected during January to May of 1988, were examined for geographic variation in morphometric characters and gill-raker counts. The Kruskal-Wallis test indicated a significant difference in the total gill-raker counts among areas. The morphometric data were adjusted by allometric formulae to remove size effects. The overall percent-correct classification rate for the five groups from the stepwise discriminant analysis, based on 12 adjusted morphometric characters, was 77.6%. This is 72.0% (Cohen's kappa statistic) better than would have occurred by chance. These results indicate significant meristic and morphological differences of yellowfin tuna from these areas, which suggests that fish from these areas represent separate groups.

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Fishery Bulletin, U.S. 89:289–297 (1991).

Yellowfin tuna *Thunnus albacares* is an epipelagic species found worldwide in tropical and subtropical oceanic regions, with a nearly continuous distribution in the Pacific Ocean from roughly 40°N to 40°S (Collette and Nauen 1983). The large-scale industrial fisheries for tuna in the Pacific Ocean landed an estimated 471 thousand metric tons of yellowfin tuna in 1985 (Joseph 1987). Fundamental to the proper management of yellowfin tuna is the elucidation of population structure. The interactions among existing, expanding, or developing fisheries on this resource cannot be assessed without this knowledge.

Morphometric studies have provided results useful for identifying marine fish stocks and describing their spatial distributions (Ihssen et al. 1981, Winans 1987). Morphometric characters, used extensively in the analysis of population structure of yellowfin tuna, indicate that there are at least three groups in the Pacific Ocean. Godsil (1948) and Godsil and Greenhood (1951) identified four stocks of yellowfin tuna in the Pacific (Japan, Hawaii, Peru, and the northeastern Pacific) from morphometric characters. Morphometric data indicate that yellowfin tuna from southeastern Polynesia, Hawaii, and Central America are different stocks (Schaefer 1955). Kurogane and Hiyama (1957) concluded from morphometric data that there are three stocks in the Pacific: western, central, and eastern. Royce (1964), however, concluded that there is an apparent cline in morphometric characters along the equator from off Costa Rica to the Caroline Islands. Suzuki et al. (1978) reviewed fisheries and biological data, including morphometric data, and concluded that there are at least three relatively independent stocks: western, central, and eastern Pacific. More recently, Schaefer (1989) showed morphometric differences between yellowfin tuna from north and south of 15°N–20°N in the eastern Pacific Ocean. With the exception of Schaefer's (1989) study, previous investigations primarily utilized univariate analyses of morphometric characters. Although geographic variation in yellowfin tuna morphology can be demonstrated in this manner, univariate analyses of single characters do not permit the classification of individual fish into discrete groups or stocks.

The objectives of the present study were to (1) assess and describe geographic variation in morphological characters and gill-raker counts of yellowfin tuna from five widely-scattered locations of the Pacific basin, (2) test the hypothesis of morphometrically distinguishable northern and southern groups in the eastern Pacific, and (3) identify the

best set of characters for group separation. I examined gill-raker counts because this meristic character appeared useful in separating groups of Pacific yellowfin tuna (Godsil and Byers 1944, Schaefer 1955). Rather than using the term "stock(s)," since it is not known whether there is a genetic component to the differences observed, I use the term "group(s)," as defined by Marr (1957), because this avoids the technicality of the degree to which genetics are involved in the differences observed.

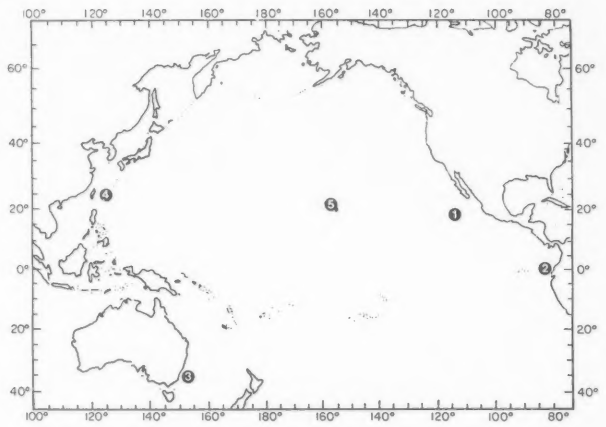



**Figure 1**
Sampling locations in the Pacific Ocean for yellowfin tuna: (1) Revillagigedo Islands, Mexico; (2) Manta, Ecuador; (3) New South Wales, Australia; (4) Ishigaki, Japan; and (5) Oahu, Hawaii.

## Materials and methods

### Sampling and data collection

Yellowfin tuna were captured by baitboats, trollers, or sportfishing boats during January to May 1988, from five localities in the Pacific Ocean: the Revillagigedo Islands, Mexico; Manta, Ecuador; New South Wales, Australia; Ishigaki, Japan; and Oahu, Hawaii (Fig. 1). These locations were selected to optimize spatial coverage within the distribution of the surface and longline fisheries for yellowfin tuna in the Pacific. Samples ranged from 66 to 105 individuals per location (Table 1), and included fish from at least four schools from each area.

**Table 1**
Summary statistics for total length in millimeters, by area, for 452 yellowfin tuna.

| Sample | $n$ | Mean | SD | Min. | Max. |
|---|---|---|---|---|---|
| Mexico | 101 | 635.4 | 151.7 | 444 | 983 |
| Ecuador | 80 | 532.9 | 101.4 | 431 | 789 |
| Australia | 66 | 853.9 | 49.4 | 690 | 990 |
| Japan | 100 | 567.9 | 142.3 | 434 | 956 |
| Hawaii | 105 | 604.7 | 87.8 | 452 | 826 |

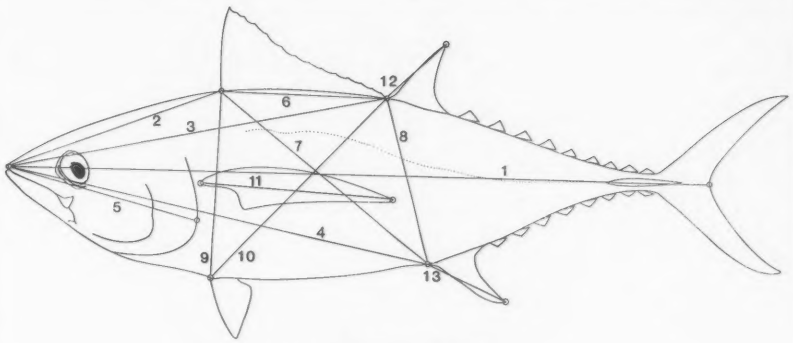
Thirteen linear measurements (Fig. 2) were made with calipers on each specimen within 24 hours of capture, and recorded to the nearest millimeter, according to methods described by Marr and Schaefer (1949). The number of gill rakers on the upper and lower limbs of the first left gill arch were also recorded for each fish. Counts for the lower limb included the single gill raker present at the angle between the upper and lower limbs (Collette and Nauen 1983). Sex was determined by examination of the gonads of the fish from Ecuador and Australia, and this subset of fish was used to test the hypothesis of no sexual dimorphism in morphometric characters of yellowfin tuna.

### Statistical analyses

Because of the variation in size of fish from different areas (Table 1), morphometric data were statistically adjusted to permit comparative analysis in terms of shape independently of size (Gould 1966, Thorpe 1983).

The morphometric measurements were first transformed to common logarithms because linearity and multivariate normality are usually more closely approximated by logarithms than by the original variables (Pimentel 1979). Outliers were detected by regression analyses of morphometric characters against total length and by scatter plots of residuals versus predicted values (Cook and Weisburg 1982). When an outlier was found, all the morphometric data (but not the gill-raker data) for that fish were withdrawn from further consideration. This procedure resulted in the elimination of morphometric data for 23 fish.

Each of the morphometric characters showed a linear relationship with total length ($r^2$ ranged from 0.95 to 0.99), when analyzed by geographic region. Analysis of covariance (ANCOVA) was employed to test for differences in allometric relationships among samples, and to estimate the common within-group regression slopes. Within-group regression slopes were significantly different ($P<0.01$) for 10 of the morphometric characters, and thus size adjustments were based on the common within-group slopes. Coefficients from the




| Acronym | Morphometric Character |
|---|---|
| TL | Total length |
| SFD | Snout to insertion of first dorsal fin |
| SSD | Snout to insertion of second dorsal fin |
| SAF | Snout to insertion of anal fin |
| HL | Head length |
| FDSD | Insertion of first dorsal fin to insertion of second dorsal fin |
| FDAF | Insertion of first dorsal fin to insertion of anal fin |
| SDAF | Insertion of second dorsal fin to insertion of anal fin |
| FDPF | Insertion of first dorsal fin to insertion of pelvic fin |
| SDPF | Insertion of second dorsal fin to insertion of pelvic fin |
| PFL | Pectoral fin length |
| SDFL | Second dorsal fin length |
| AFL | Anal fin length |

**Figure 2**
Morphometric characters measured and acronyms used for analysis of geographic variation of Pacific yellowfin tuna.

common within-group regression are used to allometrically adjust variates when between-group heterogeneity exists (Thorpe 1976, Reist 1985 and 1986). The measurements of the morphometric characters were adjusted to those expected for the overall mean total length with a modification of the allometric formula given by Thorpe (1975):

$$\hat{Y}_i = \log_{10} Y_i - [\beta(\log_{10} X_i - \log_{10} \bar{X})]$$

where
$\hat{Y}_i$ = adjusted logarithmic character measurement of the $i$th specimen,
$Y_i$ = unadjusted character measurement of the $i$th specimen,
$\beta$ = common within-group regression coefficient of $\log_{10} Y$ against $\log_{10} X$,
$X_i$ = total length of the $i$th specimen, and
$\bar{X}$ = overall mean total length.

Reist (1985) has shown that this allometric adjustment effectively removes size variation from the data he examined. This statistical approach used to remove size effects from morphometric data has been shown to be an appropriate procedure for objective analysis of the data when there is size overlap among the groups examined (Claytor and MacCrimmon 1986).

I did not adjust gill-raker counts because Spearman's rank correlation procedure indicated that there were no significant correlations between gill-raker counts and total lengths. The Kruskal-Wallis test and a nonparametric multiple comparison test (Zar 1974) were utilized to test for differences among gill-raker counts from the five areas.

I used canonical variate analysis to examine the size-adjusted morphometric data for yellowfin tuna from five locations in the Pacific Ocean. This technique, also known as multiple discriminant function analysis (Pielou 1977), is appropriate when separation of more than

two groups is desired. Canonical variates are the scores from the individual discriminant functions; that is, they are linear combinations of the original variables. The graphical display of canonical variates (for example, canonical variates 1 and 2) is useful for demonstrating differences among groups because fish that belong to the same group appear closer together on the plot than fish from different groups. Ninety-five percent confidence circles (Pimentel 1979) for group centroids can also be calculated and plotted. In addition, canonical variates can be used to examine the effectiveness of the size-adjustment procedure. Thus, canonical variates 1 and 2 were regressed against total length, and size was considered to be effectively removed if regressions were not significant (Claytor and MacCrimmon 1986).

Stepwise discriminant analysis was used to choose the combination of variables that "best" separates the groups. The resultant discriminant function was then used to classify individual fish into groups. The discriminant analysis was applied to the adjusted morphometric characters with variables entered in a forward manner using $F = 4.0$ for entering, and $F = 3.996$ for removal. The expected actual error rates of the classification function were estimated using Lachenbruch's holdout procedure (Lachenbruch and Mickey 1968, Lachenbruch 1975, Johnson and Wichern 1982). This procedure provides less biased estimates of the misclassification rate than the resubstitution method (Lachenbruch 1975). The holdout procedure, or leaving-one-out method, is based on the classification of single observations that were withheld from model development and later classified. Cohen's kappa ($\kappa$) statistic and associated 95% confidence intervals were used to determine the improvement over chance of the percent-correct classification rates (Titus et al. 1984). Given five groups, the chance of correctly classifying a single fish is 20%.

All statistical analyses were performed on a MicroVax 3500 computer. MINITAB (Ryan et al. 1976) was used to perform regression analyses and ANOVA procedures; BMDP (Dixon et al. 1981) was used to perform ANCOVA procedures and discriminant function analyses.

## Results

Data from male and female yellowfin tuna were pooled in subsequent analyses because two-sample $t$ tests for mean values of adjusted morphometric characters and gill-raker counts of fish from Ecuador and Australia indicated no significant differences between sexes (Table 2).

Total gill-raker counts and counts from the upper limb and lower limb were significantly different ($P < 0.01$) among yellowfin tuna from the five areas (Table 3). Results from the multiple comparison test for the total gill-raker-count data indicate no significant difference between the rank sums for Australia and Japan and those for Mexico and Hawaii, but these pairs are significantly different from each other and from those of Ecuador. Total gill-raker counts appeared to be a better discriminator than either the upper or lower limb counts.

The regressions for canonical variables 1 and 2 against total length ($r$ 0.17, $P = 0.14$, and $r$ 0.22, $P = 0.09$) were not significant, indicating that size effects had been removed from the morphometric variates. The plot of the first two canonical variates, which account for 57% and 26% of the total variation, shows complete separation of the centroid values for each

**Table 2**

Summary of two-sample $t$ test for differences among male and female yellowfin tuna for 12 morphometric characters adjusted for total length, and gill-raker counts, by areas. Definitions of character acronyms are given in Figure 2. None of the $t$ statistics are significant at $P = 0.05$.

| | Ecuador | | | Australia | | |
|---|---|---|---|---|---|---|
| | | Mean | | | Mean | |
| Character | $t$ | Male $n$ 45 | Female $n$ 33 | $t$ | Male $n$ 37 | Female $n$ 27 |
| SFD | 0.31 | 2.29 | 2.29 | −1.29 | 2.28 | 2.28 |
| SSD | 0.87 | 2.53 | 2.53 | 0.39 | 2.53 | 2.53 |
| SAF | 0.57 | 2.57 | 2.57 | 0.13 | 2.57 | 2.57 |
| HL | −1.01 | 2.24 | 2.24 | −0.66 | 2.23 | 2.23 |
| FDSD | −0.42 | 2.18 | 2.18 | 1.12 | 2.19 | 2.19 |
| FDAF | 0.35 | 2.37 | 2.37 | 0.78 | 2.38 | 2.38 |
| SDAF | −1.04 | 2.18 | 2.19 | −0.14 | 2.18 | 2.18 |
| FDPF | −1.00 | 2.34 | 2.34 | 0.64 | 2.35 | 2.35 |
| SDPF | −1.12 | 2.17 | 2.17 | 1.16 | 2.19 | 2.19 |
| PFL | 0.85 | 2.21 | 2.21 | −0.95 | 2.24 | 2.25 |
| SDFL | 0.94 | 1.85 | 1.84 | −1.52 | 1.91 | 1.92 |
| AFL | 1.07 | 1.83 | 1.83 | −0.92 | 1.90 | 1.90 |
| Gill rakers | | | | | | |
| Upper limb | 1.06 | 9.36 | 9.24 | 0.60 | 8.28 | 8.19 |
| Lower limb | −0.04 | 21.45 | 21.46 | −0.30 | 20.98 | 21.04 |
| Total | −0.64 | 30.74 | 30.87 | −0.81 | 29.27 | 29.48 |

**Table 3**

Gill-raker counts (means ± SD) and associated $H$ values (Kruskal-Wallis, df 4) for yellowfin tuna from five locations in the Pacific Ocean. $^*P<0.01$.

| Character | Mexico ($n$ 101) | Ecuador ($n$ 80) | Australia ($n$ 66) | Japan ($n$ 100) | Hawaii ($n$ 100) | All ($n$ 447) | $H$ |
|---|---|---|---|---|---|---|---|
| Upper limb | 8.4 ± 0.6 | 9.3 ± 0.5 | 8.2 ± 0.5 | 8.3 ± 0.6 | 8.4 ± 0.6 | 8.5 ± 0.7 | 127.18* |
| Lower limb | 21.6 ± 0.8 | 21.5 ± 0.8 | 21.0 ± 0.8 | 21.2 ± 0.8 | 21.9 ± 0.7 | 21.5 ± 0.9 | 52.20* |
| Total | 30.0 ± 1.1 | 30.8 ± 0.9 | 29.2 ± 1.0 | 29.5 ± 1.1 | 30.2 ± 1.0 | 30.0 ± 1.1 | 92.56* |

group, as indicated by the 95% confidence circles for population centroids (Fig. 3). Although there is noticeable overlap of individuals, particularly of fish from Mexico and Ecuador, the fish of the eastern Pacific (Mexico and Ecuador) are fairly distinct from those of the central (Hawaii) and western Pacific (Australia and Japan). The samples from Japan and Hawaii appear to be more similar than those from Australia and Japan. The canonical variate analyses suggest that size-adjusted morphometric characters are useful for the delineation of yellowfin tuna groups. I then used stepwise discriminant function analysis to identify the most useful characters and to estimate the classification function. The stepwise analysis revealed that 11 of the 12 adjusted morphometric characters contributed significantly to the multivariate discrimination of the five groups of fish (Table 4). The approximate $F$ statistic computed from Mahalanobis $D^2$ indicates a significant difference among the five groups ($F_{0.05}$ = 40.77, df 44,1585.8, $P<0.01$). The correct classification rates estimated from the holdout procedure for the 11-variable discriminant function ranged from 61.5 to 95.3%, with an overall rate of 77.6%, which is 72.0% ($\kappa$) better than would have occurred by chance (95% confidence intervals: $67.0\% \leqslant \kappa \leqslant 77.0\%$).

Pectoral fin length (PFL) is the single most useful character for distinguishing yellowfin tuna from the five groups (Fig. 4). Yellowfin tuna from Mexico and Ecuador can be distinguished from one another and from those from Australia, Japan, and Hawaii by this character alone (Newman-Keuls multiple range test). In addition to shorter PFL of fish from the eastern Pacific, the second dorsal fin length and anal fin length are shorter, relative to those of fish from Australia, Japan, and Hawaii. Head length, however, is shorter for fish from the western Pacific.

Because I was interested in improving the ability to delineate fish from Mexico and Ecuador, morphometric characters of these fish were readjusted and subjected to a second stepwise discriminant analysis. The common within-group slopes were used to adjust the morphometric characters to those expected for the overall mean total length for these two groups, employing the previous formula. The regression of the discriminant function score against total length was not significant ($P$ = 0.37), indicating that size effects had been removed by the adjustment procedure. The frequency distribution of the canonical variable (Fig. 5) shows fairly good separation into the two groups, with only a small amount of overlap. Results of the stepwise discriminant analysis are presented in Table 5. The correct classification rate for the fish from Mexico and Ecuador was 81.3% and 88.5%, respectively, with an overall rate of 84.6%, which is 69.3% ($\kappa$) better than would have occurred by chance (95% confidence interval: $58.3\% \leqslant \kappa \leqslant 80.3\%$). Fish from the two groups were significantly different ($F_{0.05}$ = 40.00, df 6,162, $P<0.01$).

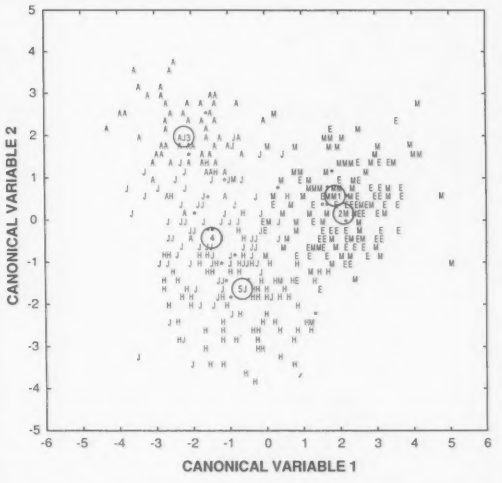



**Figure 3**

Plot of individuals, group centroids, and 95% confidence circles for population centroids on canonical variables 1 and 2 for the five groups of yellowfin tuna, based on 12 adjusted morphometric characters. Symbols for individual fish: M = Mexico, E = Ecuador, A = Australia, J = Japan, H = Hawaii. Overlap of individuals from different groups is indicated by asterisks. Symbols for group centroids: 1 = Mexico, 2 = Ecuador, 3 = Australia, 4 = Japan, 5 = Hawaii.

**Table 4**

Summary of stepwise discriminant analysis for 5 groups and 12 adjusted morphometric characters of yellowfin tuna. Character acronyms are defined in Figure 2.

| Step number | Variable entered | *F* value to enter or remove | Number of variables included | Approximate *F*-statistic | Degrees of freedom | |
|---|---|---|---|---|---|---|
| 1 | PFL | 154.39 | 1 | 154.39 | 4 | 424 |
| 2 | SDFL | 78.92 | 2 | 113.28 | 8 | 846 |
| 3 | FDPF | 47.73 | 3 | 92.76 | 12 | 1116.80 |
| 4 | SFD | 38.58 | 4 | 81.71 | 16 | 1286.81 |
| 5 | HL | 21.04 | 5 | 70.77 | 20 | 1393.93 |
| 6 | SDPF | 15.86 | 6 | 62.62 | 24 | 1462.93 |
| 7 | SDAF | 14.03 | 7 | 56.67 | 28 | 1508.54 |
| 8 | AFL | 10.24 | 8 | 51.53 | 32 | 1539.42 |
| 9 | FDSD | 8.09 | 9 | 47.20 | 36 | 1560.68 |
| 10 | FDAF | 8.01 | 10 | 43.79 | 40 | 1575.49 |
| 11 | SSD | 6.44 | 11 | 40.77 | 44 | 1585.82 |

**Classification results**

| Group | *n* | Percent correct | Number of fish classified into group | | | | |
|---|---|---|---|---|---|---|---|
| | | | Mexico | Ecuador | Australia | Japan | Hawaii |
| Mexico | 91 | 75.8 | 69 | 14 | 2 | 3 | 3 |
| Ecuador | 78 | 84.6 | 5 | 66 | 1 | 4 | 2 |
| Australia | 64 | 95.3 | 0 | 0 | 61 | 3 | 0 |
| Japan | 96 | 61.5 | 3 | 0 | 13 | 59 | 21 |
| Hawaii | 100 | 78.0 | 3 | 3 | 4 | 12 | 78 |
| Total | 429 | 77.6 | | | | | |

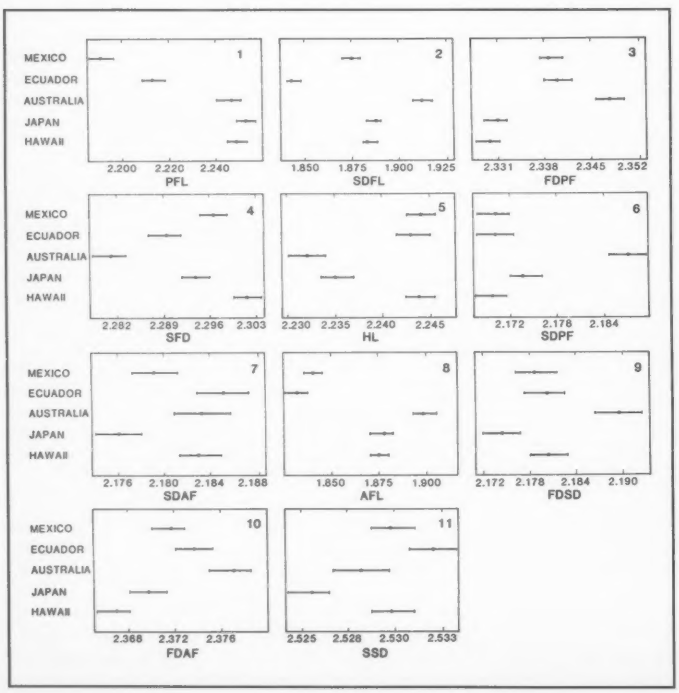



**Figure 4**

Means and individual 95% confidence intervals based on pooled standard deviations for morphometric characters adjusted for total length, for five yellowfin tuna sample areas in the Pacific Ocean, and the order in which they entered the stepwise discriminant analysis. Character acronyms are defined in Figure 2.

## Discussion

The results of these analyses of morphometric characters and gill-raker counts suggest that each of the areas included in this investigation is inhabited by a discrete group of yellowfin tuna.

Yellowfin tuna from the eastern Pacific are morphologically more similar to one another than are fish from the central and western Pacific, as shown by the amount of overlap in the samples from Mexico and Ecuador relative to those of Australia, Japan, and Hawaii (Fig. 3). The overlap of samples from the eastern Pacific may be due to a greater degree

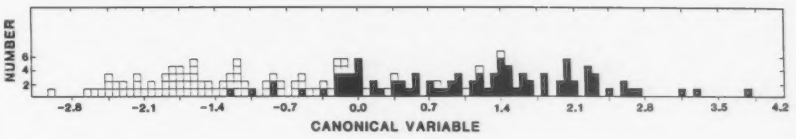



**Figure 5**

Frequency distribution of individual canonical scores based on 12 adjusted morphometric characters for yellowfin tuna from Mexico (open squares) and Ecuador (black squares). Centroid values for Ecuador and Mexico are −1.31 and 1.12, respectively.

**Table 5**

Summary of stepwise discriminant function analyses for Mexico and Ecuador groups and 12 adjusted morphometric characters of yellowfin tuna. Character acronyms are defined in Table 2.

| Step number | Variable entered | *F* value to enter or remove | Number of variables | Approximate *F*-statistic | Degrees of freedom |
|---|---|---|---|---|---|
| 1 | SDFL | 120.116 | 1 | 120.116 | 1 167 |
| 2 | PFL | 25.336 | 2 | 81.478 | 2 166 |
| 3 | SFD | 12.282 | 3 | 62.104 | 3 165 |
| 4 | SDAF | 12.988 | 4 | 53.209 | 4 164 |
| 5 | SSD | 4.730 | 5 | 44.481 | 5 163 |
| 6 | FDSD | 8.022 | 6 | 40.002 | 6 162 |

**Classification results**

| | | | Number of fish classified into group | |
|---|---|---|---|---|
| Group | *n* | Percent correct | Mexico | Ecuador |
| Mexico | 91 | 81.3 | 74 | 17 |
| Ecuador | 78 | 88.5 | 9 | 69 |
| Total | 169 | 84.6 | | |

of mixing of the groups of fish within this region. My results agree with other studies on the morphometrics of yellowfin tuna from the Pacific Ocean: morphological differences exist among fish in the eastern, central, and western Pacific (Godsil 1948, Godsil and Greenhood 1951, Schaefer 1955, Kurogane and Hiyama 1957, Royce 1964).

One of the objectives of this study was to further evaluate the previously reported morphometric differences between northern and southern groups in the eastern Pacific (Schaefer 1989). The morphometric analysis of yellowfin tuna from the eastern Pacific by Schaefer (1989) was based upon samples from 55 locations and comprised a total of 2701 fish collected during 1974–76. Only the first eight morphometric characters shown in Figure 2 of this study were recorded and included in the analyses of that investigation. The correct classification rates from the discriminant analysis of the morphometric data from yellowfin tuna sampled from north of 15°N–20°N was 68.0%, and for those sampled from the south was 73.7%; the overall correct classification rate was 72.1%. In this study two additional morphometric characters (second dorsal and pectoral fin lengths) were selected first and second in the stepwise discriminant analysis of morphometric characters of fish from Mexico and Ecuador, indicating their discriminatory power (Table 5). The correct classification rate from the discriminant analysis for these two groups was 84.6% (Table 5). The correct classification rate from the discriminant analysis for these two groups, using the eight morphometric characters (Fig. 2) investigated by Schaefer (1989), was only 68.6%.

Total gill-raker counts of yellowfin tuna appear to be important characters which permit separation of fish from the eastern, central, and western Pacific. This meristic character also has the potential for separation of fish on a latitudinal scale as clearly indicated by the

separation of fish from Mexico and Ecuador. The gill-raker counts reported by Godsil and Byers (1944) are based upon relatively few fish from several widely scattered locations in the Pacific, but show differences between fish from Japan and those from Hawaii, Ecuador, and northern Mexico. Differences in the gill-raker counts of fish from Central America and from Hawaii have been reported by Schaefer (1955).

I recommend the use of gill-raker counts for separation on a broad geographic scale. However, this character alone is not adequate for the discrimination and classification of individuals from selected geographical locations, and should thus be collected in conjunction with morphometric data to allow finer resolution within major oceanic areas. Because 11 of the 12 adjusted morphometric characters contributed significantly to the stepwise discriminant analysis (Table 4), and because none of the 13 characters (Fig. 2) are potentially difficult to measure, I consider the set of 13 characters utilized in this study to be appropriate for future investigations of tuna morphometrics.

Extensive tagging studies designed to investigate movements of yellowfin tuna have been conducted only in the eastern Pacific (Joseph et al. 1964, Bayliff 1979, Hunter et al. 1986). Movements of yellowfin tuna in the eastern Pacific tend to be restricted, with few individuals moving more than several hundred miles. Tagging of yellowfin tuna during 1968–74 in the eastern Pacific, in inshore and offshore areas, indicated few long-distance east-west or north-south movements of the fish. The results of the present study and that of Schaefer (1989) on morphometrics of yellowfin tuna in the eastern Pacific also suggest that movements are restricted. The results of this investigation appear to be in reasonably good agreement with those of tagging studies, although several tagged yellowfin tuna released in the central Pacific have been recaptured in the eastern Pacific, and a tagged yellowfin tuna released in the western Pacific was recaptured in the eastern Pacific after traveling a net distance of 3806 miles (Peterson 1983).

Observed morphometric and meristic differences in this investigation are probably influenced both by genes and environment. It would be valuable to conduct a study of the population structure of yellowfin tuna throughout the Pacific; morphometric and meristic data should be collected, along with tissue samples to be analyzed for genetic information. Both mitochondrial DNA and nuclear genes should be screened and analyzed (Avise 1987). This approach would address the genetic basis of the groups inferred from morphometric and meristic differences. The accumulated information from morphometrics, meristics, and genetics, along with other life-history information, could then be evaluated for a better understanding of the population structure of yellowfin tuna in the Pacific Ocean.

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**Abstract.**—Fecundity of the yellow rock crab *Cancer anthonyi* was examined seasonally over two years. Ovigerous crabs varied in size from 89 to 153 mm carapace width. Crabs held in the laboratory brooded more than three clutches per year without molting or mating. Crab fecundity varied seasonally, with peaks in late spring–early summer and late fall–early winter. Ovigerous crabs carried an estimated 0.73–3.30 million eggs, depending on crab size, stage of egg development, and season. The log body size–log fecundity relationship changed significantly with crab embryogenesis. Estimates of reproductive potential, defined in terms of the total number of eggs produced throughout the entire adult life span, were based on the mean number of eggs produced at the mean adult size, the minimum and maximum number of mature instars, the minimum and maximum number of broods per instar, and the number of broods oviposited per year. For a female *C. anthonyi*, it was 14.7–29.4 million eggs, which was relatively higher than other members of the genus.

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# Fecundity and the Reproductive Potential of the Yellow Rock Crab *Cancer anthonyi*

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The yellow rock crab *Cancer anthonyi* Rathbun, 1897, supports a growing fishery in southern California. The rock crab fishery exceeds 600 tons annually ($2 million ex-vessel value), with the Santa Barbara district representing 40–60% of the total catch (Resource Agency of California 1981–87, Carroll and Winn 1988). Three species of rock crabs comprise the fishery (*C. antennarius*, *C. anthonyi*, and *C. productus*), with *Cancer anthonyi* being most prevalent in catches in southern California (Winn 1985, Carroll and Winn 1988). At present, rock crabs are exploited with no restrictions on sex or reproductive condition; ovigerous and nonovigerous females are both removed by the fishery.

Little is known about the reproductive biology of most *Cancer* species (for review, see Shields 1991). We investigated fecundity and aspects of the reproductive biology of *Cancer anthonyi* as part of a larger study that examined brood mortality resulting from nemertean predation (Shields et al. 1990). We report observations on multiple broods per crab and interbrood periods, and present an analysis of crab fecundity in relation to size, embryogenesis, and seasonality. Lastly, we define reproductive potential in terms of the maximum lifetime fecundity of an individual crab, and compare reproductive potential within the genus.

## Methods

Ovigerous female crabs were trapped by a commercial fisherman at depths of 10–100 m from the Santa Barbara Channel, between Summerland and Gaviota, California (approximately 34°23′–34°25′N, 119°34′–120°12′W). Twenty to twenty-five female crabs were obtained at monthly or bimonthly intervals for two years (November 1981–November 1983). We sampled 345 ovigerous *Cancer anthonyi* of which 311 were completely processed (see Shields et al. 1990). Carapace width (CW) was measured, and the entire second left pleopod was excised and stored in 5% formalin in seawater for further analyses. Crabs were then released or maintained in flowing seawater aquaria for additional observations.

Embryogenesis was examined by observing embryos throughout the developmental process. The time to eclosion, interbrood period, and the effect of temperature on embryogenesis were examined in crabs maintained in aquaria with running seawater at normal oceanic temperatures. Crabs maintained in aquaria were fed market squid or mackerel weekly or biweekly. For statistical analyses, broods were grouped on the basis of the embryogenic development of attached eggs; i.e., embryos were in early (I–II), middle (III–IV), or late (V–VII) stages of development, or near hatching (VIII). Roman numerals refer to the developmental stages of embryogenesis (EDS) of Shields and Kuris (1988a) and Shields et al. (1990).

The term fecundity is here defined as the total number of live eggs carried by each female at any given time during incubation. Fecundity per pleopod was estimated as in Shields et al. (1990); it represents the number of live eggs on the 2d left pleopod. In addition, the actual fecundity per crab was determined for 12 crabs (96 pleopods). The fecundities of other crabs were then estimated using the regression of fecundity/pleopod with the fecundity of the 12 crabs.

Statistical analyses (ANOVA, ANCOVA, linear regression, Sidak's inequality) were conducted with the aid of SAS (1982). The log-transformation was used to reduce differences in variance between groups. A value of $P<0.05$ was accepted as significant. Data from all of the 2d left pleopods were statistically independent. Two statistics were used to minimize the influence of outliers on the analysis of covariance of log fecundity and log size between seasons, and between EDS groups. An outlier was removed from the ANCOVA and the subsequent regression analyses only if the value of its studentized residual was ± 1.50, the value of its Cooke's D influence statistic was greater than 0.006 (SAS 1982), and only if these statistics were consistent between transformed and untransformed data (5 outliers in early and middle embryogenesis). We suggest that the 5 outliers were bearing a second or third brood between molting and mating events, hence their fecundity was low (see below).

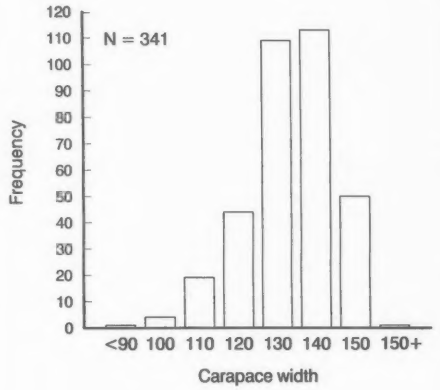


**Figure 1**
Size-frequency histogram of ovigerous *Cancer anthonyi* by 10-mm increments.

**Table 1**
Brood and interbrood period (days) for three groups of *Cancer anthonyi* females. Crabs were trapped while ovigerous, and the initial interbrood period was recorded after eclosion. All values are expressed as means ( ± SD); $N$ = number of crabs. Numbers of crabs decreased within each group as a result of mortality.

| Group | Brood | Days | Temp. (°C) | $N$ | Interbrood | Days | Temp. (°C) | $N$ |
|---|---|---|---|---|---|---|---|---|
| A | I | 40.7 ± 3.1 | 14.6 ± 1.1 | 16 | I | 42.9 ± 20.5 | 14.3 ± 0.7 | 16 |
| | II | 33.7 ± 4.1 | 16.6 ± 1.5 | 11 | II | 49.4 ± 18.1 | 15.3 ± 1.2 | 12 |
| B | I | 51.8 ± 4.4 | 10.9 ± 1.9 | 13 | I | 45.9 ± 28.4 | 10.5 ± 1.3 | 15 |
| | II | 38.2 ± 3.5 | 13.1 ± 1.0 | 12 | II | 25.1 ± 5.2 | 12.6 ± 1.5 | 10 |
| | III | 45.6 ± 5.8 | 12.4 ± 0.9 | 9 | III | 48.0 ± 27.5 | 12.5 ± 0.7 | 10 |
| C | I | 35.8 ± 3.8 | 14.9 ± 1.8 | 8 | I | 26.9 ± 9.6 | 14.1 ± 0.7 | 8 |
| | II | 34.3 ± 3.1 | 16.2 ± 1.6 | 3 | II | 55.0 ± 30.5 | 15.1 ± 1.6 | 7 |
| Total | | 40.0 ± 6.6 | 14.1 ± 2.1 | | | 41.9 ± 11.5 | 13.5 ± 1.6 | |
| | | Range (29–58) | | | | Range (16–123) | | |

## Results

### General observations

Ovigerous females varied from 89 to 153 mm in carapace width (Fig. 1), with a mode at 140 mm. Broods of *C. anthonyi* were oviposited without observed prior mating or molting by the female crab, and were observed for every mature crab held in the laboratory; some crabs brooded at least three clutches per year in the laboratory (Table 1). At a mean seawater temperature of 15°C, crab eggs took approximately 40 days to develop from oviposition to eclosion (Table 1). Subsequent broods were typically produced within 1–2 months after eclosion of the previous brood. Crab embryos from subsequent broods (second and third) were viable and hatched normally. In addition, the seminal receptacles of 24 crabs that were dissected after the eclosion of at least a second brood contained viable spermatozoa.

Broods oviposited in sand- and gravel-bottomed aquaria were smaller than those from crabs in the field (mean fecundity/pleopod = $2.75 \pm 0.73$(SD) $\times 10^5$, versus $4.10 \pm 0.67$ (SD) $\times 10^5$; $N = 12$ and 12, respectively; $t = 4.72$, $P < 0.001$); but food or holding effects may have confounded ovarian development and fecundity in lab-held crabs.

*Cancer anthonyi* brooded an estimated 0.73–3.30 million eggs per clutch depending on crab size. Crab fecundity (log fecundity/pleopod) was significantly different between broods in different stages of embryogenesis (Table 2; ANOVA, Sidak's inequality, $P < 0.05$). Clutch size did not differ significantly between broods in early and middle stages of development, hence these broods were combined for the size-fecundity analyses.

At eclosion, female crabs actively aided the hatching process. Females stood upon all of their legs and vigorously aerated their brood by agitating their abdomens and pleopods. Water currents through the gill chamber appeared to reverse their usual direction and flowed anteriorly through the egg mass. This facilitated eclosion, and pushed hatched prezoeae out of and away from the clutch. Within 2–3 days after hatching, female crabs stripped their pleopods of empty and dead eggs. The setae of cleaned pleopods attained a golden sheen comparable to their appearance on a freshly molted crab.

**Table 2**

Changes in log fecundity/pleopod with embryogenesis. EDS refers to developmental stages of embryogenesis [class 1, EDS I–II; class 2, EDS III–IV; class 3, EDS V–VII; class 4, EDS VIII] (Shields and Kuris 1988a, Shields et al. 1990). Days of development are based on temperatures of 15°C. Values with different letters are significantly different (ANOVA, Sidak's inequality, $P < 0.05$).

| EDS class | Days of development | $N$ | Fecundity/pleopod (log no. of eggs) ± SD | |
|---|---|---|---|---|
| 1 | 1–12 | 97 | 5.504 ± 0.200 | A |
| 2 | 13–30 | 129 | 5.517 ± 0.201 | A |
| 3 | 31–38 | 78 | 5.399 ± 0.239 | B |
| 4 | 39–40 | 31 | 4.748 ± 0.421 | C |

### Size-fecundity relationship

The fecundity per pleopod (log) was positively correlated with crab size (log CW) ($R$ 0.521, $P < 0.001$, $N$ 219; Fig. 2), but fecundity per crab (log) was not

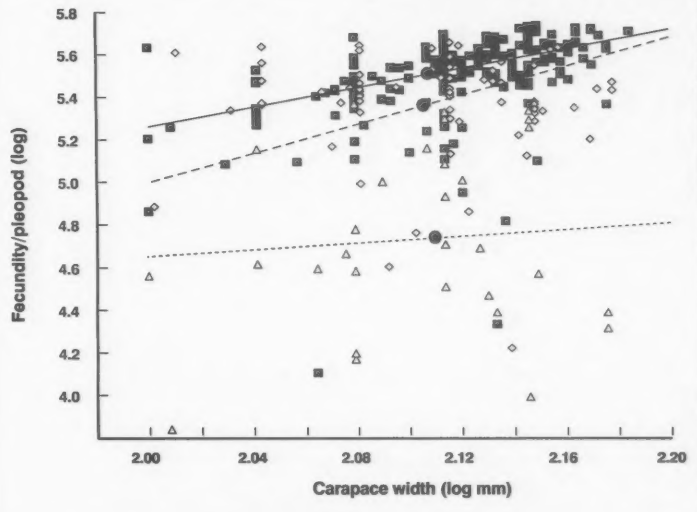


**Figure 2**

Size (CW)–fecundity relationships for *Cancer anthonyi* with broods in different stages of embryogenesis. Fecundities of crabs with eggs in early and middle stages of embryogenesis (boxes, solid line) and late embryogenesis (diamonds, dashed line) were highly correlated with crab size (in early and middle EDS, log fecundity/pleopod = 2.135(log CW) + 1.015, $R = 0.521$, $N = 219$; in late EDS, log fecundity/pleopod = 3.321(log CW) + 1.637, $R = 0.544$, $N = 70$; $P < 0.001$ for both). Fecundities of crabs with eggs near hatching (triangles, dotted line) were not correlated with size (log fecundity/pleopod = 0.723(log CW) + 3.217, $R = 0.055$, $N = 30$, $P > 0.05$). See text for ANCOVA results.

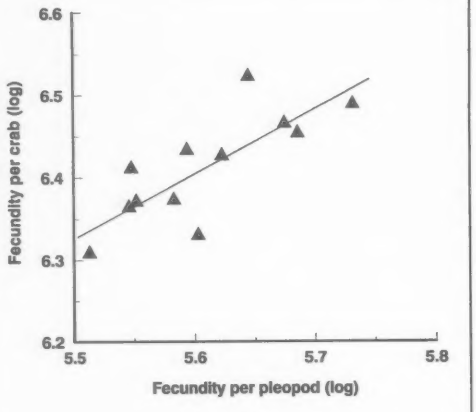


**Figure 3**

Relationship between fecundity per pleopod (X) and fecundity per crab (Y) for 12 crabs (log Y = 2.124 + 0.765 log X, $R = 0.782$, $N = 12$, $P<0.01$). The regression equation was used to calculate fecundity per crab for estimates of reproductive potential for *Cancer anthonyi*.

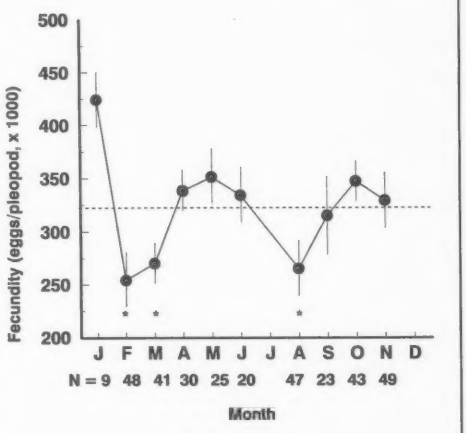


**Figure 4**

Seasonal variation in the fecundity per pleopod of *Cancer anthonyi*. Months with significantly less fecundity than other months are denoted with an asterisk (ANOVA, Sidak's inequality, $P<0.05$). Bars represent standard error of the mean; $N$ = sample size; dashed line = mean fecundity.

correlated with crab size ($R$ 0.449, $P>0.05$, $N$ 12). The partial correlation of fecundity with crab size was significant when fecundity per pleopod was held constant (partial correlation: $R$ 0.635, $P<0.05$, $N$ 12). Thus, projections of reproductive potential (based on estimates of the fecundity per crab) were derived from the correlation of fecundity per pleopod with fecundity (Fig. 3).

In addition, the relationship between fecundity per pleopod and crab size was significantly influenced by embryogenesis (Fig. 2). Slopes of the regressions and adjusted mean fecundities were significantly different between EDS groups (ANCOVA, adjusted means, $F_{(2,315)} = 224.57$, $P<0.01$; separate slopes, $F = 62.71$, $P<0.01$). Fecundity was not correlated with crab size when hatching was imminent (Fig. 2).

### Seasonal relationships

Crab fecundity varied seasonally (Fig. 4). Fecundity data from both years were combined for the seasonal analysis since their seasonal patterns were similar (ANOVA, log transformation, between years, within months, $P>0.05$). In February, March, and August, the mean fecundity/pleopod was lower than at other times of the year (ANOVA, log transformation, Sidak's inequality by month, $P<0.01$). The differences in mean fecundity/pleopod cannot be attributed to differences in crab size (CW) or developmental stage (EDS) during those months (two-way ANOVA with interaction, $P>0.05$, n.s.); they represent seasonal fluctuation in crab fecundity.

The size-fecundity relationship was significantly affected by seasonality. Crabs in late-winter and late-summer months (February, March, and August) brooded significantly fewer eggs than crabs of similar size in other months (ANCOVA, adjusted means of log fecundity/pleopod = $5.522 \pm 0.012$ (SE) versus $5.564 \pm 0.006$, respectively, $P<0.0025$). The slopes of the regression of log size on log fecundity/pleopod were also different between seasons (ANCOVA, separate slopes analysis, $b_{winter-summer} = 1.556$ versus $b_{spring-fall} = 2.573$, $P<0.001$). While these data show significant statistical variations, their biological significance remains speculative.

## Discussion

Most *Cancer* crabs carry a single brood through a single reproductive season. While multiple ovipositions after a single mating have been reported, they generally occur in two or more reproductive seasons (Williamson 1904, Knudsen 1964, Krouse 1972, Haefner 1976, Ebert et al. 1983). Indeed, multiple ovipositions during a single reproductive season have only been reported for *C. anthonyi* (this study), *C. antennarius*

(Shields, Okazaki, and Kuris, pers. observ.), and *C. productus* (Knudsen 1964).

Ovigerous *Cancer anthonyi* occur throughout the year in southern California. The proportion of ovigerous females in the female crab population varied seasonally, with a peak in the number of ovigerous crabs in March and a nadir in the ovigerous population in June (Reilly 1987). Crab fecundity, however, followed an opposite pattern. *Cancer antennarius*, which has a geographic range similar to *C. anthonyi*, bears eggs throughout the year with a peak in reproduction during the winter months (Carroll 1982).

Ovigerous *C. anthonyi* were highly fecund. Although body size and fecundity are highly correlated in the Brachyura (Hines 1982), for *Cancer* the larger crabs *C. magister* and *C. pagurus* bear relatively fewer eggs than *C. anthonyi* (Table 4). Differences in fecundity may be partially explained by differences in egg and zoea I size, and the duration of embryogenesis (Table 3), which in turn may be explained by climatic regime (Hines 1986). While the data remain incomplete, we note two general patterns: (1) Some species of *Cancer* produce many small eggs (higher fecundity) that quickly develop into small larvae, and (2) some species produce relatively larger eggs (lower fecundity) that slowly develop into large larvae.

Decreases in fecundity per pleopod during embryogenesis are mostly a result of nemertean predation or mechanical abrasion (Shields et al. 1990). The decrease is apparently related to crab size; larger crabs appear to lose relatively fewer eggs throughout embryogenesis than do smaller crabs. The impact of nemertean predators on the fecundity of the shore crab *Hemigrapsus oregonensis*, was also greater on smaller crabs (Shields and Kuris 1988b). While smaller crabs may be more numerous in a population (e.g., Gutierrez and Zuniga

**Table 3**

Comparative features of embryogenesis (diapause, D), egg size (widest diameter), length of zoea I, duration of larval development (zoea I to megalopae), female size at maturity, and fecundity for ten species of *Cancer*. Unknown data are indicated (?).

| Species | Embryogenic development (in days) | Egg diameter (μm) | Zoea I length* (mm) | Larval development (in days) |
|---|---|---|---|---|
| *C. antennarius*[1] | 50–60 | ? | 1.3 | ? |
| *C. anthonyi*[2] | 29–58 | 265–300 | 1.2 | 33–45 |
| *C. borealis*[3] | ? | 305 | 1.2 | ? |
| *C. gracilis*[4] | ? | ? | 1.2 | ? |
| *C. irroratus*[5] | 176–235 (*D*) | ? | 1.5 | ? |
| *C. magister*[6] | 90–120 | 400–440 | 2.5 | 45–160 |
| *C. oregonensis*[7] | 103–118 | ? | ? | ? |
| *C pagurus*[8] | 235–265 (*D*) | 450–500 | 1.8 | 35+** |
| *C productus*[9] | ~120 | ? | 1.8 | ~95 |
| *C. setosus*[10] | ? | 450 | ? | ? |

*Length of zoea I is carapace vertex to telson tips. Data from Ingle (1981).
**Does not include duration of megalopa stage.

References: [1]Carroll 1982, Shields et al. unpubl. data; [2]This study, Anderson and Ford 1976; [3]Haefner 1977, Carpenter 1978; [4,7,9]Knudsen 1964; [4,6,7,9]Orensanz and Gallucci 1988; [5]Shotton, 1973, Krouse 1976, Haefner 1976, Reilly and Saila 1978, Campbell and Eagle 1983; [6]Wild 1983abc, Hankin et al. 1985, Shirley et al. 1988; [8]Edwards 1979, Brown and Bennett 1980, Nichols et al. 1982, Le Foll 1986; [9]Toole 1985; [10]Gutierrez and Zuniga 1976.

**Table 4**

Range in size of ovigerous females, number of broods per instar, maximum number of adult instars, estimated range in fecundity per brood, and individual reproductive potential in various *Cancer* crabs. Unknown data are indicated (—), incomplete data (?), and numbers in parentheses represent the potential number of broods in later instars. For key to references, see Table 3.

| Species | Size (mm CW) | Broods per instar | Max. avg. no. adult instars | Est. range in fecundity per brood | Individual reproductive potential (eggs) |
|---|---|---|---|---|---|
| *C. antennarius*[1] | 116–143 | 1–2 | 5 | $\sim 1.0 \times 10^6$ | $5.0–10.0 \times 10^6$ |
| *C anthonyi*[2] | 90–153 | 2–3 | 3–4 | $0.7–3.3 \times 10^6$ | $14.7–29.4 \times 10^6$ |
| *C. borealis*[3] | 105–135 | 1 (?) | — | $0.3–1.6 \times 10^6$ | — |
| *C gracilis*[4] | 54–100 | 1 (2) | 2 | ? | — |
| *C. irroratus*[5] | 21–100 | 1 | 1–6? | $4.4–567.7 \times 10^3$ | $1.7–2.1 \times 10^6$ |
| *C. magister*[6] | 110–170 | 1 (2) | 3–4 | $0.5–1.5 \times 10^6$ | $3.0–4.0 \times 10^6$ |
| *C. oregonensis*[7] | 10–43 | 1 (2) | 6 | $1.0–3.3 \times 10^4$ | $<0.2 \times 10^6$ |
| *C. pagurus*[8] | 133–205 | 1 (3) | 3? | $0.5–3.0 \times 10^6$ | $5.3–8.7 \times 10^6$ |
| *C. productus*[9] | 70–129 | 1 (2) | 3 | ? | — |
| *C. setosus*[10] | 83–151 | 1 (?) | 2–3? | $0.6–1.7 \times 10^6$ | $2.3–3.5 \times 10^6$ |

1976, Hankin et al. 1985), their overall contribution to the production of planktonic larvae may be relatively equal to or less than that of the less-abundant larger females whose eggs may have a greater chance of surviving embryogenesis.

*Cancer anthonyi* has a high reproductive potential (Table 4). Estimates of reproductive potential are typically based on the growth, size at maturity, longevity, and fecundity of an animal (Campbell and Robinson 1983). These estimates have been applied to animals having but a single brood per year. Here, we define reproductive potential for an animal capable of producing more than one brood per year (reproductive potential: mean number of eggs produced at mean adult size, minimum and maximum number of mature instars, minimum and maximum number of broods per instar, and the estimated number of broods per year). We use the **maximum** or **entire** adult life span because (1) late instar females may contribute most to the overall egg production of their cohort, (2) estimates of adult mortality are unknown for most species, and (3) confounding correlations between fecundity and mortality are eliminated (Shields 1991). While admittedly crude, the estimates of reproductive potential are useful for comparisons (Table 4). The reproductive potential of a single female *C. anthonyi* was estimated at 14.7–29.4 million eggs in her lifetime (2.6 million eggs/brood at mean size, 3–4 broods/year, 2–4 reproductive years). *Cancer magister* has an estimated potential of approximately 3–5 million eggs (1–1.5 million eggs/brood, 1 brood/year, 3 reproductive years; MacKay 1942). Neither of these estimates consider smaller broods from older instars or variations in brood size within an instar.

Most *Cancer* crabs breed but once a year, making study of their reproduction and reproductive habits logistically difficult. The high fecundity and great reproductive potential of *Cancer anthonyi*, coupled with its frequent production of eggs, may provide an excellent model for the study of reproduction in *Cancer* crabs.

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## Citations

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# Robustness of the Wetherall Length-based Method to Population Disequilibria

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**Abstract.**– For fish populations in equilibrium, estimates of Z/K and $L_\infty$ can be obtained solely from length-frequency data by using the Wetherall length-based method. Robustness of this method to departures from equilibrium conditions is examined with a population simulation model. During disequilibrium conditions following either the initiation of a fishery or a 1-year perturbation in recruitment, estimates of both parameters, especially Z/K, are severely biased. Three-year averaging of catch length-frequencies does not substantially reduce this bias. A test, based on the chi-square statistic, is proposed for detecting population disequilibrium. Provided that the sizes of length-frequency samples are sufficiently large, the test is an effective way to detect population disequilibrium and thereby avoid biased parameter estimates.

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Assessments of tropical fish stocks have increasingly turned to length-based methods rather than the more traditional age-based methods, because of the difficulty in ageing tropical fishes (Pauly and Morgan 1987). Although all length-based methods use length-frequency data, they are designed to measure different biological parameters and vary in their requirements for additional types of data. Wetherall et al. (1987) examined one class of length-based methods—those designed to estimate both growth and mortality parameters without the need for additional data—and developed two new estimators: a maximum likelihood estimator and a regression estimator. The second estimator, because of its simplicity, has received the most widespread use (Wetherall 1986, Arellano 1989, Polovina 1989, Rawlinson 1989).

The regression estimator of Wetherall et al. (1987), henceforth referred to simply as the Wetherall method, estimates two parameters. The first ($\Theta$) is the ratio of the instantaneous total mortality rate (Z) to the rate constant of the von Bertalanffy growth function (K). The second ($L_\infty$) is the asymptote of the von Bertalanffy growth function. These parameters are estimated by regressing the mean length ($\bar{l}_i$) of all fish $\geq l_{ci}$ on $l_{ci}$, a cutoff length ranging from the first length category that is fully selected by the fishery ($L_c$) to the largest length category. Estimates of Z/K and $L_\infty$ are then calculated as $Z/K = B/(1 - B)$ and $L_\infty = A/(1 - B)$, where A is the intercept and B is the slope of the regression.

Like many other length-based methods, the Wetherall method requires the population to be in equilibrium, a condition often not fulfilled because of variations in both the environment and the fishery (Csirske et al. 1987, Ralston 1989). Although Wetherall et al. (1987) clearly have cautioned potential users that biases may result if populations are in disequilibria, the likely magnitudes of such biases have not been addressed. This has prompted us to investigate the sensitivity of the method to two common types of perturbations: (1) a rapid increase in effort during the fishing-up stage of a fishery, and (2) a fluctuation in recruitment. In this paper, we examine the temporal patterns and magnitudes of biases associated with these disequilibria and present a simple statistical test that can be used with catch length-frequencies to detect population disequilibria and help minimize the consequent potential for biased parameter estimates.

## Materials and methods

The performance of the Wetherall method can be assessed by applying it to catch length-frequencies generated by a length-based population simulation model that accounts for growth, mortality, and recruitment. The model is configured to

simulate a population of opakapaka *Pristipomoides filamentosus*, a Hawaiian deepwater snapper. Mean length-at-age ($L_t$) is described by a von Bertalanffy growth equation:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}); \quad (1)$$

where $L_\infty$, K, and $t_0$ are parameters. Estimates for these parameters ($L_\infty$ = 66 cm, K = 0.24/year, and $t_0$ = −0.78 year) are from Ralston and Miyamoto (1983). As a computational convenience, however, growth is considered an incremental process:

$$L_t = L_1 + \sum_{i=1}^{t-1} DL_i, \quad (2)$$

where the annual growth increment ($DL_t$) is expressed as a time-differenced form of Equation (1):

$$DL_t = L_{t+1} - L_t = L_\infty e^{-K(t-t_0)} (1 - e^{-K}). \quad (3)$$

Variance in length-at-age ($V_t$) is described by an asymptotic function of age:

$$V_t = C(1 - e^{-Dt}), \quad (4)$$

where C and D are parameters. Estimates of these parameters can be obtained by fitting this function to size and age data obtained from Ralston and Miyamoto (1983), but the predicted variance is unrealistically large. Consequently, the parameters C = 10 and D = 0.1 are chosen to best fit the predicted-to-observed length-frequency distributions. Variance in annual growth increment is described as a time-differenced form of Equation (4):

$$DV_t = V_{t+1} - V_t = C(1 - e^{-D}) e^{-Dt}. \quad (5)$$

Recruitment is assumed to occur instantaneously at age-1 and, unless experimentally manipulated, to be identical each year. The length distribution of recruits is assumed to be normal with a mean and variance defined by Equations (1) and (4), respectively. The length distribution of the surviving members of this age-class in subsequent years (y) is estimated with the recursive relationship:

$$N_{l,t+1,y+1} = \sum_{s=l_0}^{l} N_{s,t,y} e^{-(M+QF)} P(l - s|t); \quad (6)$$

where M and F are the instantaneous rates of natural and fishing mortality, Q is a size-dependent selectivity coefficient, $l_0$ is the smallest individual in each age group and $P(l - s|t)$ is the conditional probability of growing an amount $(l - s)$ at t years of age. The growth-increment probability function is assumed to be normal with a mean and variance computed from Equations (3) and (5). An estimate of natural mortality (M = 0.3) is obtained from Ralston (1987); estimates of fishing mortality (F = 0.3 and 0.6) are chosen somewhat arbitrarily to bracket the probable true value for opakapaka. The selectivity coefficient Q is represented by a reparameterized logistic function of length:

$$Q = \frac{1}{1 + e^{-E(l - l_{50})}}, \quad (7)$$

where E is a parameter controlling the steepness of the function, and $l_{50}$ is a parameter controlling the length of 50% selectivity. The parameter values of E = 0.5 and $l_{50}$ = 45 cm are chosen arbitrarily. The population length-distribution is calculated by summing across all age-classes, i.e.,

$$N_{l,.,y} = \sum_t N_{l,t+1,y}, \quad (8)$$

and the catch length-frequency distribution is calculated as

$$C_{l,.,y} = N_{l,.,y} \left( \frac{QF}{M+QF} \right) (1 - e^{-(M+QF)}). \quad (9)$$

The parameters Z/K and $L_\infty$ are estimated from the simulated catch length-frequency distribution as follows. First, the length at full vulnerability ($L_c$) is estimated as one length interval (1 cm) larger than the rightmost mode in the catch length-frequency distribution (Polovina 1989). Second, $\bar{l}_i$, the mean length of all fish $\geq l_{ci}$, is calculated for each $l_{ci} > L_c$. Third, $\bar{l}_i$ is regressed on $l_{ci}$ by using weighted linear regression with weights equal to the sample size (i.e., $\Sigma C_l$ for $l > l_c$). Fourth, Z/K and $L_\infty$ are then computed from the previously specified functions of the regression coefficients.

The disequilibrium experiments are conducted as follows. For the experiments examining the fishing-up phase of a fishery, the initial population length-frequency distribution is set at the equilibrium distribution in the absence of fishing. This length distribution is generated by running the model with F = 0.0 until the population is in equilibrium (i.e., until the total population size is identical on two successive iterations). Fishing mortality at each of the two specified levels is then applied instantaneously, and the simulation is run until the population is again at equilibrium. For the experiments examining the effect of perturbation dur-

ing recruitment, the initial population length-frequency distribution is set at the equilibrium distribution with a fishery producing F = 0.6. Two types of recruitment perturbations are tested: (1) a year with twice the normal recruitment, and (2) a year with a complete absence of recruitment. After each recruitment perturbation is introduced, the simulation is run until the population is again in equilibrium. Since disequilibrium bias may be only one component of the total bias of a parameter, the disequilibrium bias is isolated by expressing it as a percentage difference relative to the equilibrium value rather than the known value of a parameter.

Population equilibrium is statistically tested by comparing a catch length-frequency distribution in any one year to those from the previous two years by using a chi-square test of independence. Rationale for this type of test is that a population in equilibrium should, except for sampling variability, produce catch length-frequencies that are identically distributed over time. Significance of the chi-square test therefore indicates that the population is not in equilibrium. Performance of the chi-square test first requires the construction of 3-by-N frequency tables, where N is the number of size categories that are jointly defined over the 3-year sequence. To do this, the largest and smallest size categories in the catch containing at least five individuals in each of the three years are determined. Then for each year, all size categories less than the lower bound of the joint interval are pooled, as are all size categories greater than the upper bound. Once the table is constructed, the chi-square test can be performed according to the procedures described in Conover (1971).

The statistical power of the test is examined in a Monte Carlo experiment in which the test is applied to catch length-frequencies generated by the population simulation model. For each disequilibrium experiment, annual catch length-frequencies are subsampled, with replacement, with subsample sizes of 100, 500, 1000, and 5000 fish. At each level of subsampling, a chi-square test of independence is then performed on each 3-year sequence of subsampled length-frequencies. Subsampling and testing are replicated 100 times, and the power is estimated as the proportion of the 100 tests that is significant at the 5% level.

To determine whether disequilibrium bias could be reduced by averaging a series of catch length-frequencies over time, the Wetherall method is also applied to simulated catch length-frequencies after they have been time-averaged. First, the catch length-frequencies for each year are converted to proportions by length. Second, the time-series of catch proportions for each size interval is smoothed by using a 3-year centered running average. Third, the smoothed catch proportions at length for each year are then multiplied by the actual catch (in numbers) for that year to recover the true sample size.

In addition to disequilibrium bias, also examined are two types of bias that can influence Wetherall estimates of Z/K and $L_\infty$ even when the population is in equilibrium. The focus of this examination is on the variation in these biases as a function of the chosen value of $L_c$. To do this, the model first is run until equilibrium conditions are reached. Then for each chosen value of $L_c$, the Wetherall method is applied to the catch length-frequency distribution, which experiences size selection by the fishery, and to the population length-frequency distribution. Type I bias in the estimates of Z/K is expressed as the percentage difference between the estimates based on catch length-frequencies and those based on population length-frequencies. Type II bias in the estimates of Z/K is expressed as the percentage difference between the estimates based on population length-frequencies and the known values of Z/K.

## Results and discussion

As Wetherall et al. (1987) have cautioned, population disequilibrium indeed leads to biased estimates of Z/K and $L_\infty$, but the temporal pattern and magnitude of this bias vary greatly with the type of equilibrium perturbation. In the fishing-up experiment, disequilibrium bias in the estimates of Z/K is initially large and negative, but later becomes positive before decaying to zero (Fig. 1a). Increasing the fishing mortality rate increases the magnitude of the positive bias and shortens the time in which the maximum positive bias is reached. The magnitude of fishing mortality, however, appears to have little effect on the magnitude of the initial negative bias. Disequilibrium bias in the estimates of $L_\infty$ changes with time and with fishing mortality rate in a manner similar to the bias in Z/K, but the bias in $L_\infty$ is almost always positive and considerably smaller than the bias in Z/K (Fig. 1b). In the recruitment perturbation experiment, when recruitment is doubled for 1 year, the disequilibrium bias in the estimates of Z/K is oscillatory in time and has a pronounced positive peak and a less-pronounced negative peak (Fig. 1c). When recruitment is eliminated for 1 year, the disequilibrium bias in Z/K is again oscillatory, but the positive and negative peaks occur 2 years later and the magnitude of the bias, especially that of the negative bias, is smaller. Disequilibrium bias in $L_\infty$ varies with time in a manner similar to the bias in Z/K, but again the bias is smaller in magnitude (Fig. 1d). Thus, the following two points emerge from these simulations: (1) Biases in both parameters can be large but vary tremendously as the size structure of the

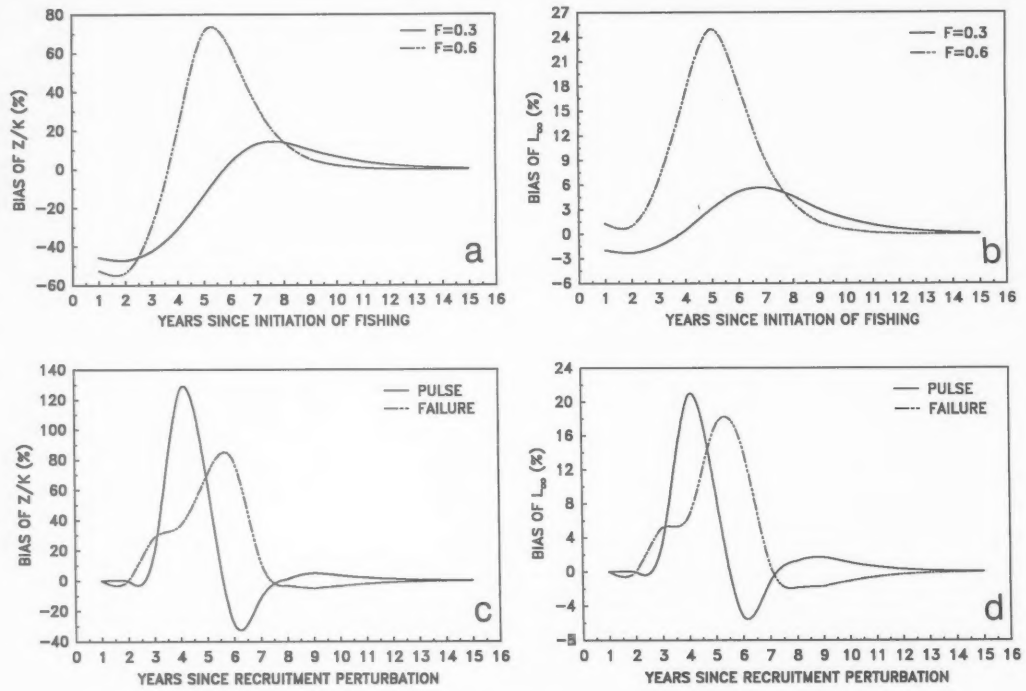


**Figure 1**

Temporal patterns of disequilibrium bias in the estimates of Z/K and $L_\infty$, expressed as percentage differences relative to the equilibrium values. For the fishing-up experiment at two fishing mortality rates (F = 0.3 and 0.6), biases of (a) Z/K and (b) $L_\infty$ are plotted against the number of years since the initiation of the fishery. For the recruitment perturbation experiment at F = 0.6, biases of (c) Z/K and (d) $L_\infty$ are shown plotted against the number of years since a 1-year doubling of recruitment (pulse) and a 1-year absence of recruitment (failure).

population adjusts from one equilibrium to the next, and (2) bias in Z/K estimates is considerably larger than bias in $L_\infty$ estimates.

Even though the simulated changes in fishing mortality and recruitment may be more abrupt than those typically experienced by the population, the simulations clearly demonstrate that the Wetherall estimates of Z/K and $L_\infty$ can be quite biased when the population is not in equilibrium. As a consequence, the method apparently can be used with confidence only when population equilibrium can be demonstrated. Such a demonstration of equilibrium, or lack thereof, can be achieved by comparing successive catch length-frequencies with a chi-square test of independence. The utility of the chi-square test can best be judged by examining its statistical power to detect the disequilibrium conditions that lead to biased parameter estimates. Since the statistical power of the proposed test will increase as between-year differences in catch length-frequencies increase, it will tend to vary positively with the magnitude of parameter bias. Provided that sample sizes are sufficiently large, the test can therefore be used as a data screening device to detect when parameter bias is likely. One important consideration, then, is the relationship between sample size and the undetectable level of disequilibrium bias. This relationship can be seen by comparing the time trajectories of power (Fig. 2) with those of bias (Fig. 1).

Consider first the fishing-up experiment and bias in estimates of Z/K. For F = 0.3 and a sample size of 5000 fish, the statistical power of detecting disequilibria is high (i.e., $\geq 0.75$) from years 3 to 7 (Fig. 2a). Although this interval includes most of the period in which bias is high (Fig. 1a), it does not include the first 2 years after the initiation of the fishery when bias is also high, because the proposed test requires 3 successive years of data. Furthermore, the interval of high statistical power does not include years 8–10 when bias is nearly

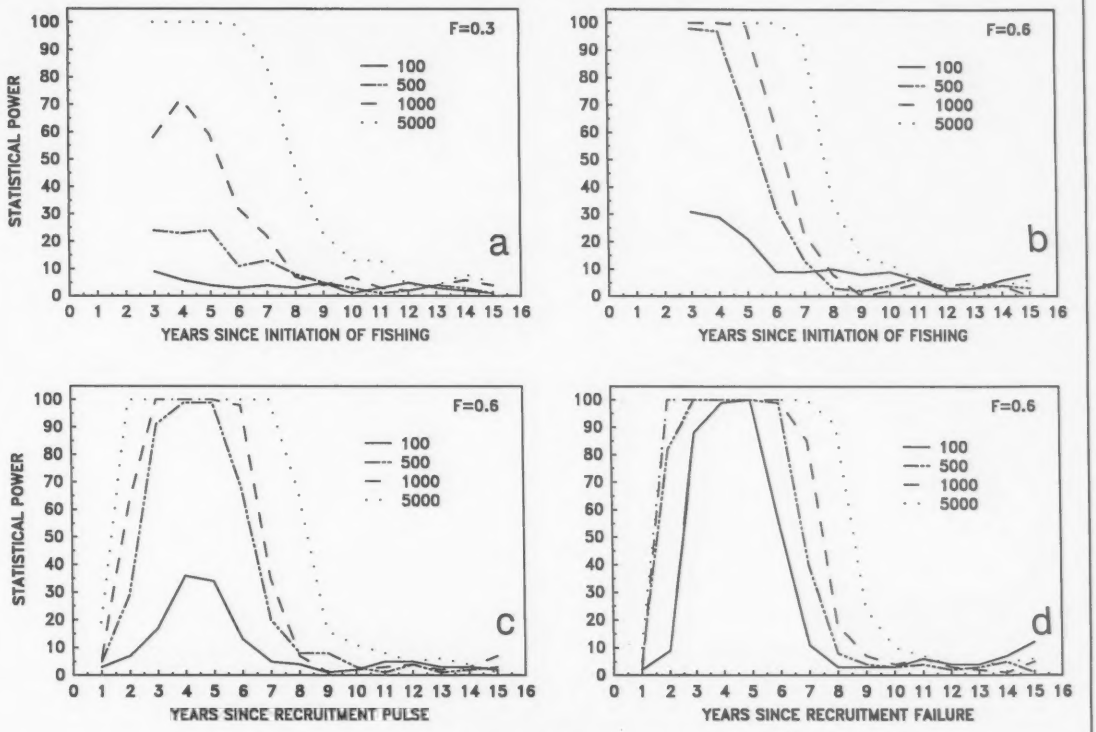


**Figure 2**

Temporal patterns in the statistical power of a chi-square test to detect population disequilibrium at each of four levels of sampling ($N$ = 100, 500, 1000, and 5000). For the fishing-up experiment, power is shown for (a) F = 0.3 and (b) F = 0.6, starting in the third year after the initiation of the fishery and continuing to equilibrium. For the recruitment perturbation experiment at F = 0.6, power is shown for (c) the 1-year doubling of recruitment and (d) the 1-year absence of recruitment starting in the year in which the perturbation occurred and continuing to equilibrium.

13%. For F = 0.6 and a sample size of 5000 fish, the interval of high power is almost identical to that at F = 0.3. At lower sample sizes, however, the chi-square test is considerably more powerful when F = 0.6 than when F = 0.3.

In the recruitment perturbation experiment, statistical power is high over a broader time-interval than in the fishing-up experiment. For the case of a 1-year doubling of recruitment at a sample size of 5000 fish, power is high between years 2 and 8, an interval that includes the entire period in which disequilibrium bias is >5%. For the case of a 1-year absence of recruitment, power is high between years 2 and 8, an interval that again includes the entire period in which disequilibrium bias is >5%. Unlike the situation in the fishing-up experiments, power tends to remain relatively high with reductions in sample size. These experiments indicate that, in terms of its ability to detect the likelihood of disequilibrium bias, the chi-square test performs best on a 1-year doubling of recruitment, second best on a 1-year absence of recruitment, and worst on the fishing-up disequilibrium. The fishing-up case is worst because the test cannot be applied to the first 2 years of the time-series when bias is high and larger sample sizes are needed to detect disequilibrium.

In addition to the type of disequilibrium perturbation and size of the length-frequency sample used, the statistical power of the chi-square test also varies with the number of length-distributions included. Thus, power is calculated for tests including two, three, and four length-distributions. Since the gain in power is substantial when the number of length-distributions is increased from two to three but only minor when the number is increased from three to four, all further power simulations are based on three length-distributions.

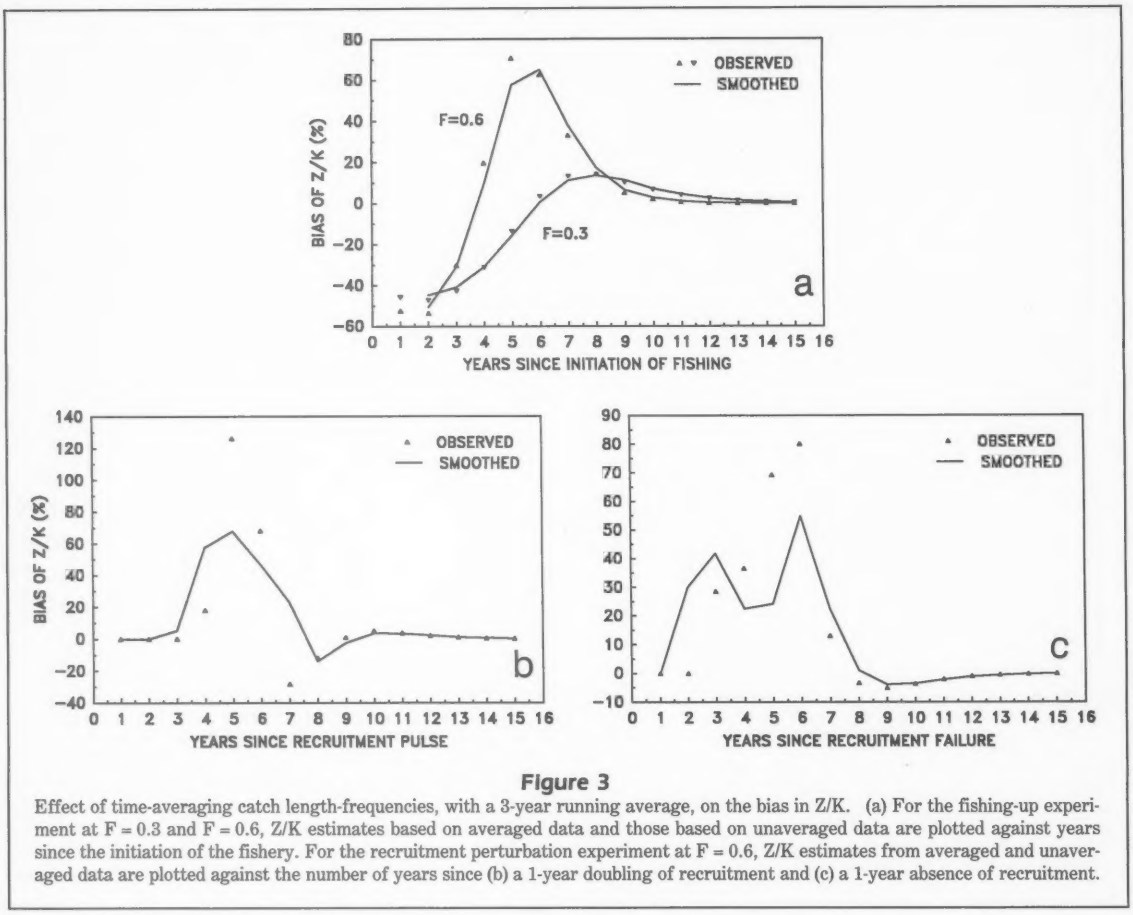


**Figure 3**

Effect of time-averaging catch length-frequencies, with a 3-year running average, on the bias in Z/K. (a) For the fishing-up experiment at F = 0.3 and F = 0.6, Z/K estimates based on averaged data and those based on unaveraged data are plotted against years since the initiation of the fishery. For the recruitment perturbation experiment at F = 0.6, Z/K estimates from averaged and unaveraged data are plotted against the number of years since (b) a 1-year doubling of recruitment and (c) a 1-year absence of recruitment.

If a population is found to be in disequilibrium, one can either discard the parameter estimates or find some means to reduce or eliminate the disequilibrium bias. Following the second approach, we have examined the utility of a technique often used with such age-based procedures as catch curve analysis to reduce the effects of year class variability. This technique consists of averaging the catch length frequencies over time. The effectiveness of time-averaging depends on the type of perturbation that creates the disequilibrium. In the fishing-up experiment, time averaging has essentially no effect when F = 0.3 and only a slight effect when F = 0.6 (Fig. 3a). In the recruitment variation experiment, time averaging has a somewhat greater effect, especially during the periods of maximum bias when reductions in bias are as much as 30% (Fig. 3b). Time averaging, however, also increases bias during some periods. Although time averaging is somewhat more effective when disequilibrium is due to recruitment perturbation, the 3-year time averaging employed in our study appears to be an ineffective way of reducing disequilibrium bias.

Besides disequilibrium bias, the Wetherall method is subject to two types of biases that may occur even when the population is in equilibrium. The first type of equilibrium bias (herein referred to as Type I or selection bias) is always negative and occurs when fish, equal in length to the smallest $l_c$ values used in the regression, are not fully vulnerable to the fishery (Fig. 4a). Since, in practice, the exact form of the fishery selection curve will rarely be known, choice of the initial $l_c$ value is somewhat arbitrarily based on the shape of a catch length-frequency histogram. Our approach follows Polovina (1989) in choosing the initial $l_c$ to be one size-interval greater than the rightmost mode on a length-frequency histogram. This choice, however, can result in selection bias. For example, when F = 0.3, the initial $l_c$ (51 cm) is identical to the length of 95%

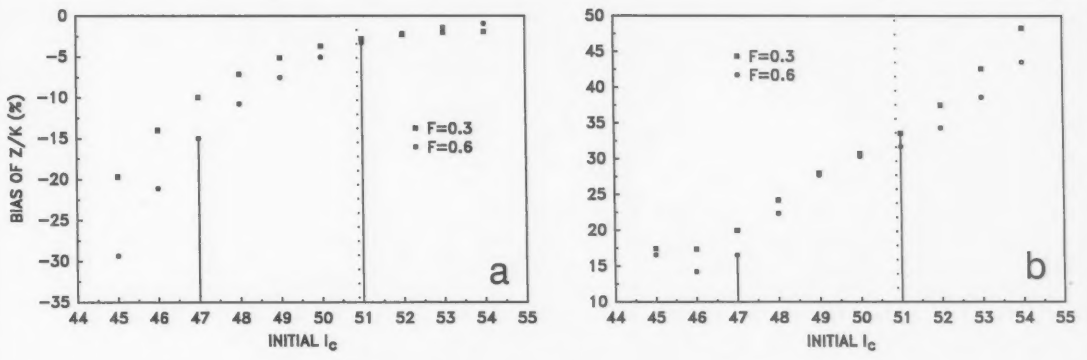


**Figure 4**

(a) Selection bias (i.e., bias due to inclusion in the Wetherall method of fish lengths that are incompletely selected by the fishery) and (b) residual bias (i.e., equilibrium bias that cannot be explained by selection) are shown as functions of the initial value of $l_c$. The $l_c$ values (calculated as one size-interval larger than the rightmost mode in the catch length-frequency distribution) are shown as solid vertical lines at 47 cm for F = 0.6 and at 51 cm for F = 0.3. The size of 95% selection is shown with a vertical dotted line at 51 cm.

selection, and selection bias is small (3%). But when F = 0.6, the initial $l_c$ (47 cm) is considerably less than the size at 95% selection, and selection bias is consequently larger (15%).

Since selection bias asymptotically approaches zero with increasing value of the initial $l_c$ (Fig. 4a), one logical way of reducing equilibrium bias would be to choose a larger initial $l_c$. This strategy, however, would increase the second type of equilibrium bias (herein referred to as Type II or residual bias), because residual bias increases with initial $l_c$ (Fig. 4b). For example, when F = 0.6 and the initial $l_c$ = 47 cm, residual bias is about 16%. But when F = 0.3 and $l_c$ = 51 cm, residual bias is 34%. Although the causes of residual bias are unknown, it could be related to either of two factors. First, as Wetherall et al. (1987) demonstrate, the estimates of Z/K and $L_\infty$ are asymptotically unbiased as the sample size increases. Since increasing the size of the initial $l_c$ reduces sample size, it follows that bias will increase. Second, as Laurec and Mesnil (1987) demonstrate, individual variability in growth, which has been incorporated into our simulation model, leads to bias in length-based estimates of mortality.

In the foregoing, we have demonstrated that disequilibrium bias in the Wetherall estimates of Z/K and $L_\infty$ can be large and that time averaging does not remove such

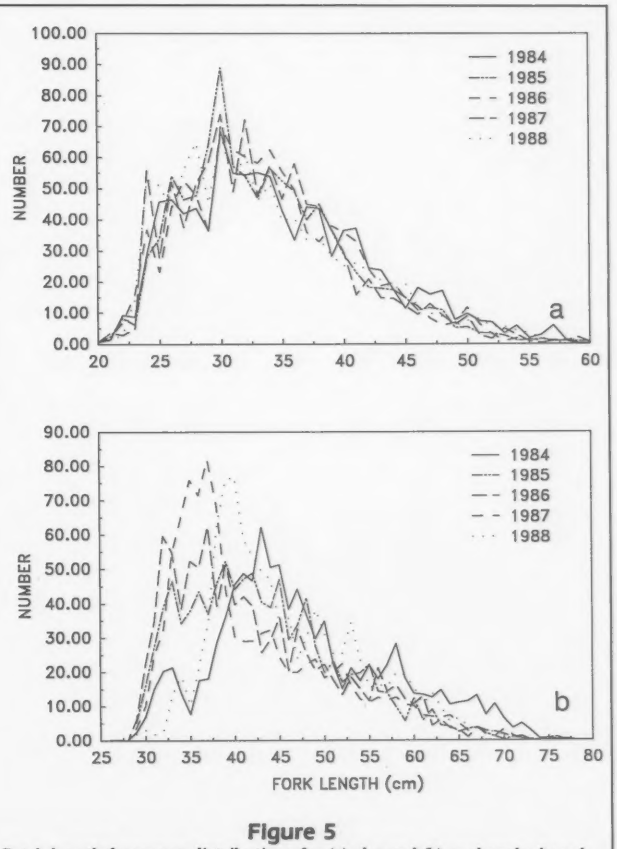


**Figure 5**

Catch length-frequency distributions for (a) ehu and (b) opakapaka based on 3000 fish samples collected in each year (1984–88).

bias. In light of this, the general utility of the Wetherall method clearly depends upon whether fish populations actually reach equilibrium, or conditions close enough to equilibrium, so that the consequent bias will be small. We believe, however, that equilibrium conditions may prevail more frequently than generally perceived. For example, ehu *Etelis carbunculus*, another deepwater snapper caught by Hawaii's bottomfish fishery, displays considerably less variability in size between years than opakapaka. Chi-square tests, performed on annual length-frequency samples of 3000 fish collected in 1984–88 (Fig. 5), are always not significant for ehu (1986, $P = 0.19$; 1987, $P = 0.40$; 1988, $P = 0.11$) but are always highly significant for opakapaka (1986–88, $P < 0.001$). Therefore, the ehu population is apparently close enough to equilibrium that using the Wetherall method would be appropriate. In general, however, the Wetherall method should be used with extreme caution on new or changing fisheries or species experiencing recruitment fluctuations. In all cases, its use should be preceded by a statistical verification of population equilibrium.

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# Movement Patterns and Stock Affinities of King Mackerel in the Southeastern United States

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**Abstract.**–King mackerel *Scomberomorus cavalla* were tagged and released from southeastern Florida, the Florida Keys, and South Carolina from 1975 through 1979 to document spatial and temporal movement patterns. Distance traveled by tagged king mackerel was not significantly related to size (fork length), but was correlated with number of days-at-large. King mackerel show a cyclical pattern of movement along the Atlantic seaboard of the southeastern United States and coastal waters of the Gulf of Mexico. A migratory behavior may exist in which fish return to the area of release over a period of up to 5 years. The number of fish moving away from the area of release and their direction of movement depend on whether the fish are associated with Atlantic or Gulf waters. Some king mackerel may be residents in southeastern Florida waters. The seasonal overlap between the two recognized stocks of king mackerel in southeastern Florida is estimated to be as high as 29.4–41.8%.

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Historically, the king mackerel *Scomberomorus cavalla* has supported important recreational and commercial fisheries in the southeastern United States (Finucane et al. 1986, Brusher and Palko 1987). Concern over declining king mackerel abundance has resulted in state and federal regulation of recreational and commercial king mackerel fisheries. As part of the management strategy of this resource, two migratory groups ('stocks') of king mackerel have been established for the southeastern United States (SE U.S.): an Atlantic stock and a Gulf of Mexico stock (Williams and Godcharles 1984). From 1 November through 31 March, the range for the Gulf stock includes the entire Gulf of Mexico, extending up the Florida east coast to the Volusia/Flagler county line (Fig. 1, line A). Fish found north of this line are considered to be Atlantic stock. From 1 April through 31 October, the boundary for the Gulf/Atlantic stocks is the Collier/Monroe county line on Florida's west coast (Fig. 1, line B). A 'transition' zone, therefore, is created along the southern Florida coast (Fig. 1, shaded area).

Stock definitions were largely generated from a cooperative tagging program by the Florida Department of Natural Resources (FDNR) and National Marine Fisheries Service (NMFS) to study king mackerel resources in the SE U.S. Although these data have been utilized in various resource assessments by state and federal agencies, little of this information has been formally published. In this paper, we describe the tag returns with respect to temporal and spatial movement patterns and stock affinities of *S. cavalla*.

## Materials and methods

A total of 12,493 fish were tagged in four spatial/temporal regions along the SE U.S. from 1975 through 1979 (Table 1, Fig. 1). King mackerel were captured by fishermen, under contract to FDNR, using hook-and-line. Biologists from FDNR measured fork length (FL) of the fish and examined them for any debilitating injuries. Fish in good condition were placed ventral-side-up in a wet tagging cradle covered with plastic and foam rubber. A 7- to 10-mm longitudinal incision was made along the anterior portion of the abdomen permitting the insertion of an internal anchor tag with an external plastic streamer. Tagged fish were returned to the water, usually within 25–35

seconds after dehooking. Latitude, longitude, and condition of each release were recorded.

The tagging program was publicized through posters, newspaper and magazine coverage, and contacts with fishermen and fish dealers. To enhance returns, tag numbers were randomly selected for rewards of $5, $10, or $25. Recreational anglers and commercial fishermen were encouraged to provide the following information with each return: date, latitude and longitude, fork length, weight, sex, and type of recapture gear.

An accurate description of the length of each tagged and recaptured fish was needed to examine the relationship between size and movement. To determine whether particular length categories were disproportionally reported, we used chi-square tests to compare the length distributions (50 mm FL intervals) of all released fish with the length-at-tagging of recaptured fish for each of the four tagging regions. Length-at-tagging for recaptured fish was used because accuracy of recaptured-fish length measurements could not be determined and because the effects of growth prior to recapture were unknown and could bias the comparisons.

Temporal recapture relationships were determined by grouping returns into seven subareas for each of the four tagging regions along the SE U.S. (Fig. 1): South Atlantic Bight (SAB = Georgia, South Carolina, and North Carolina); northeastern Florida (NEFL = Georgia/Florida line to north side of Cape Canaveral); southeastern Florida (SEFL = north side of Cape Canaveral to Monroe/Dade line); the Florida Keys (FK = Monroe/Dade to Monroe/Collier line); southwestern Florida (SWFL = Monroe/Collier line to Apalachee Bay); the northeastern Gulf (NEG = Apalachee Bay to Mississippi River); and the northwestern Gulf (NWG = Mississippi River to Texas/Mexico border). Subareas for this analysis were chosen to provide as much resolution as possible given the distribution of tags and recaptures. Current stock

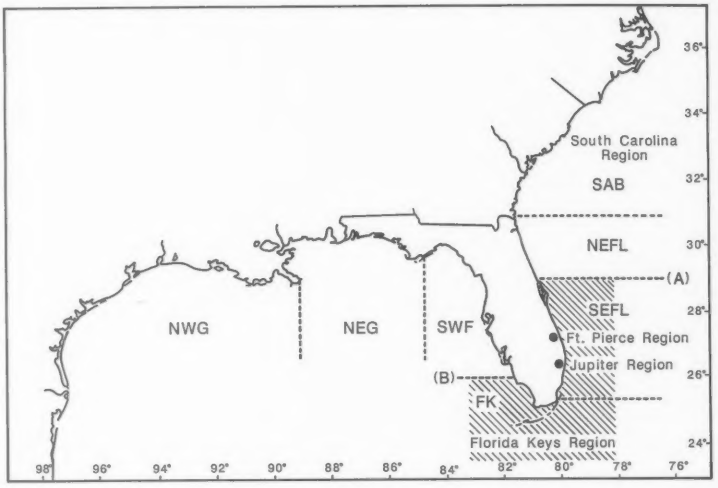


**Figure 1**

Location of seasonally shifting boundaries (labeled A and B) of the two stocks of king mackerel in the southeastern United States. The 'transition' zone formed by these two lines is outlined by the shaded area. Recapture subareas as defined in the text are also given (dashed lines).

**Table 1**

Number of king mackerel tag releases, by year.

| | Location and month of release | | | |
|---|---|---|---|---|
| Year | South Carolina[1] May, June | Ft. Pierce[2] December–March | Jupiter[3] May, June | Florida Keys[4] February, March |
| 1975 | — | 880 | 372 | — |
| 1976 | — | 1904 | 1318 | 974 |
| 1977 | — | 1666 | 588 | 844 |
| 1978 | — | 1966 | 396 | 776 |
| 1979 | 809 | — | — | — |
| Total | 809 | 6416 | 2674 | 2594 |

[1] Northern boundary of release area defined by 33°50.0′N latitude, and southern boundary by 32°03.0′N latitude.

[2] For all years, except 1975, annual totals for the Ft. Pierce area include December releases of the previous year. Northern boundary of release area defined by 28°45′N latitude and southern boundary by 27°07′N latitude.

[3] Northern boundary of release area defined by 27°07′N latitude and southern boundary by 26°19′N latitude.

[4] Eastern boundary of release area defined by 81°10′W longitude, southern boundary by 24°10′N latitude, western boundary by 83°30′W longitude, and northern boundary (Gulf of Mexico, only) by 27°00′N latitude.

definitions were considered in combination with other published king mackerel studies (e.g., Brusher and Palko 1987, Trent et al. 1987) to formulate possible subareas. The larger subareas (Fig. 1) reflect little or no tag releases and few returns, while the smaller subareas along south Florida were utilized for locations of directed tagging efforts. Returns in each subarea were sorted by year and month of recapture. A continuous time-scale, representative of the relative time of freedom and independent of actual year of release or return, was created for each subarea by designating the first 12 months after release as year 1, the second as year 2, and continuing for up to 3–5 years. Therefore, fish released in May of 1975, 1976, 1977, or 1978, for example, would be assigned a May, year-1 release date.

The spatial patterns of king mackerel returns were categorized according to the relative direction of movement through coastal SE U.S. waters rather than according to strict compass headings, because fish were released and recaptured on both the Atlantic and Gulf coasts. Fish were considered to be moving 'Atlantic-ward' if they were recaptured in Atlantic waters north of their release location or if they had moved toward the Atlantic from a release location in the Florida Keys region. Individuals were classified as moving 'Gulf-ward' if they were recaptured south of their release area or in the Gulf of Mexico. However, fish released from the Florida Keys region had to be recaptured north of the Monroe/Collier county line (B in Fig. 1) to be classified as moving Gulf-ward. Distance from tagging location was determined for each tag return. Returns were grouped into 50-km increments (i.e., 0–49 km, 50–99 km, etc.) when within 800 km of their release site and in 100-km blocks thereafter. This created a continual distance gradient for fish moving either Gulf-ward or Atlantic-ward from each of the four tagging regions. The 100-km increments were used since only 9.5% of the recaptures occurred more than 800 km from the release sites.

The relative magnitude of movement for tagged fish moving at least 100 km away from each release location, either Gulf-ward or Atlantic-ward, was determined by plotting the cumulative percentage of fish moving through, or recaptured in, each respective distance block. A 100% value was given to the block nearest the tagging area (either Atlantic- or Gulf-ward) because all fish had to move at least 100 km to be included in the analysis. The 100-km limit was used to prevent including in the analysis fish that were exhibiting random movement patterns associated with the release locations. Since measurements of fishing effort (commercial and recreational) and catchability were not available for the time-frame of our study, we had to assume that the number of returns was a reflection of relative effort. We based this assumption on the migratory nature of this species (Beaumariage 1973, Collette and Russo 1984), knowing that fishermen target king mackerel as they become available along various coastal waters.

Stock definitions for king mackerel in the southern Atlantic and Gulf of Mexico management zones were evaluated using a discriminant function technique based on a measure of generalized squared distance (SAS 1985). The classification variable used in the analysis was membership, based on when and where a specific fish was released, of the fish in either the Atlantic or Gulf stock. Number of days at large, distance from release to recapture locations, and month and location of recapture were used as quantitative variables. A test of the homogeneity of within-covariance matrices was made to determine whether the within- or pooled-covariance matrix would be used in the discriminant function. The percentage of posterior probability of classification of each return for its original stock (i.e., Atlantic or Gulf), calculated as part of this discriminant function test, was used as an indicator of the affinity of a king mackerel for its nominal stock group. The two king mackerel stocks were then divided into five substocks to refine the indices of stock affinities. The Atlantic stock was separated into two substocks: a combination of the SAB and NEFL subareas that form the SE U.S. Atlantic coast substock; and the southern Florida summer substock, which is a conglomerate of the SEFL and FK subareas from April through October. The Gulf stock was divided into three substocks: the southeastern Florida winter substock that consists of the SEFL subarea from November through March; the Florida Keys winter substock, which corresponds to the FK subarea from November through March; and a combination of all Gulf of Mexico subareas (NEG and NWG subareas) that form the combined Gulf substock. King mackerel from a one-time tagging effort off the Texas coast during 1977 ($N$ 319) by FDNR were included in the stock affinity analysis as part of those fish released as combined Gulf substock. These Texas fish were not included in any of the other analyses of the 12,493 tagged fish.

## Results

Fish length did not influence movement and was not a factor in the probability of recapture. Neither length-at-tagging ($r$ 0.08; df 1,147; $F$ 0.722) nor length-at-return ($r$ 0.075; df 1,654; $F$ 3.688) was significantly correlated with the distance that a fish traveled from its release area. Bias associated with tag return relative to length was examined by comparing length of re-

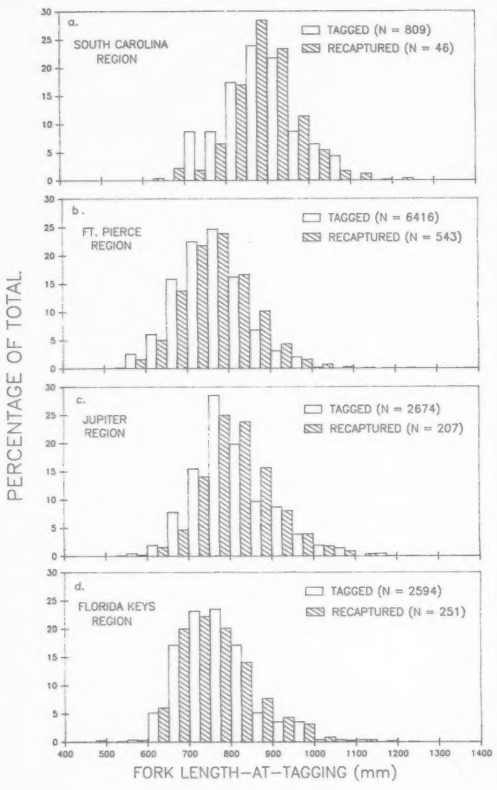


**Figure 2**

Length-frequencies at release and subsequent length-at-tagging of recaptured king mackerel from the four tagging regions. Fish were grouped by 50-mm FL interval; mid-range values are used for each plot.

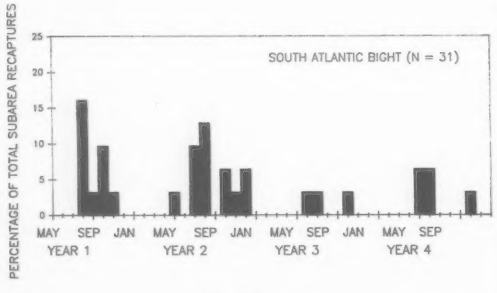
SOUTH ATLANTIC BIGHT (N = 31)
PERCENTAGE OF TOTAL SUBAREA RECAPTURES
MAY SEP JAN MAY SEP JAN MAY SEP JAN MAY SEP
YEAR 1 YEAR 2 YEAR 3 YEAR 4

**Figure 3**

Monthly return percentage of king mackerel released from South Carolina region and recaptured in the South Atlantic Bight (SAB) subarea, using a continuous time-scale representative of relative time of freedom. Returns begin with May of year 1.

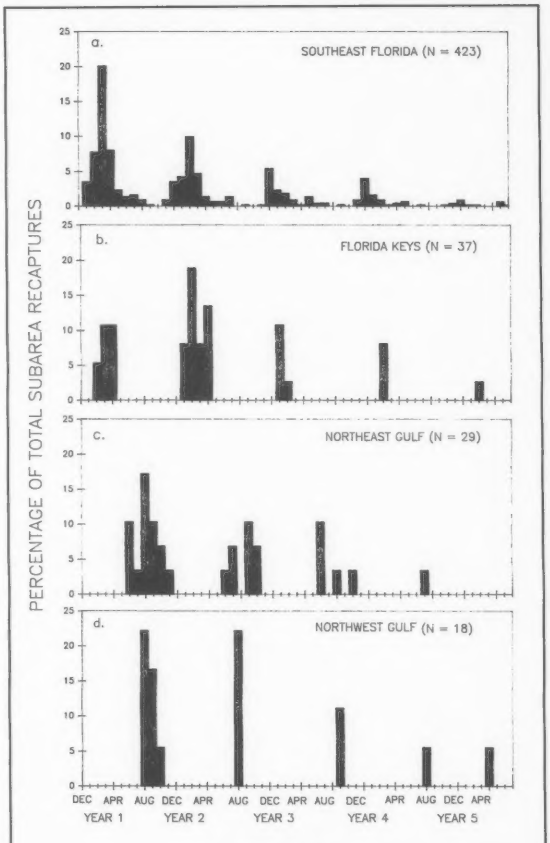
a.
SOUTHEAST FLORIDA (N = 423)
b.
FLORIDA KEYS (N = 37)
c.
NORTHEAST GULF (N = 29)
d.
NORTHWEST GULF (N = 18)
PERCENTAGE OF TOTAL SUBAREA RECAPTURES
DEC APR AUG DEC APR AUG DEC APR AUG DEC APR AUG DEC APR
YEAR 1 YEAR 2 YEAR 3 YEAR 4 YEAR 5

**Figure 4**

Monthly return percentage of king mackerel released from Ft. Pierce region and recaptured in the (a) southeastern Florida (SEFL), (b) Florida Keys (FK), (c) northeastern Gulf (NEG), and (d) northwestern Gulf (NWG) subareas, using a continuous time-scale representative of relative time of freedom. Returns begin with December of year 1.

leased fish and length-at-tagging of recaptured fish (Fig. 2a–d). No significant differences in lengths were noted for fish from any of the four tagging regions (South Carolina, $\chi^2$ 13.05, $0.25<P<0.50$, df 13; Ft. Pierce, $\chi^2$ 19.14, $0.25<P<0.50$, df 16; Jupiter, $\chi^2$ 18.76; $0.25<P<0.50$, df 16; and Florida Keys, $\chi^2$ 8.83, $0.90<P<0.95$, df 17).

## Temporal recapture patterns

King mackerel released from the South Carolina region (809 tagged; 46 returned) generally returned to the SAB subarea (*N* 31) from June through August and from October through November of each recapture

year (Fig. 3). Insufficient returns in the other SE U.S. subareas precluded further analysis of the fish released from the South Carolina region.

King mackerel released from the Ft. Pierce region (6416 tagged; 543 returned) were recaptured in all seven subareas; numbers in four subareas were adequate to describe temporal trends (Fig. 4a–d). Peak periods of recapture in the SEFL subarea (*N* 423) occurred from December through March, with a smaller peak from May through July (Fig. 4a). The number of recaptures was highest during the first recapture year, progressively decreasing from year 2 through year 5. Fish recaptured in the FK subarea (*N* 37) from the Ft. Pierce tagging region (Fig. 4b) also showed a strong annual cycle of recapture from winter through early spring, generally following the peak recaptures from SEFL by 1–3 months. A bimodal annual cycle was noted for fish recaptured in the NEG subarea (*N* 29; Fig. 4c); the first cycle occurred during June and July, and another occurred from August through October. In NWG waters (*N* 18), returns of fish tagged in the Ft. Pierce region occurred most frequently from July through August (Fig. 4d).

The regularity of seasonal increases in tag returns from fish released in each of the Ft. Pierce region subareas indicates a predictable movement pattern. Fish move progressively through SEFL and FK waters in the late-winter and early-spring and travel to the northern Gulf of Mexico subareas during warmer spring and summer months. King mackerel then complete the cycle in late-summer and early-fall by returning to their release sites. This pattern of movement may occur over a period of 3–5 years. Whether all fish participate in this movement as part of an annual event is unknown.

Recaptures of fish released in the Jupiter region (2674 fish tagged; 207 returned) were concentrated in the SEFL and FK subareas (Fig. 5a–b). The temporal return pattern from SEFL (*N* 127; Fig. 5a) was not well defined; fish were returned in all months (most during May and June), although not in every year. The lack of a seasonal return pattern may be indicative of a year-round resident population of king mackerel in this subarea. An annual, cyclical trend for returns in the FK (*N* 25) was noted during winter months, with the magnitude of this trend decreasing over a 3-year recapture period (Fig. 5b).

King mackerel released from the Florida Keys region (2594 tagged; 251 returned) were recaptured often enough to allow a description of temporal return patterns in four subareas (Figs. 6a–d). Fish were recaptured in the SEFL subarea (*N* 34) from July through September, as well as from December through March (Fig. 6a). Recaptures in the Keys subarea (*N* 166) suggested an annual trend of returns during February and

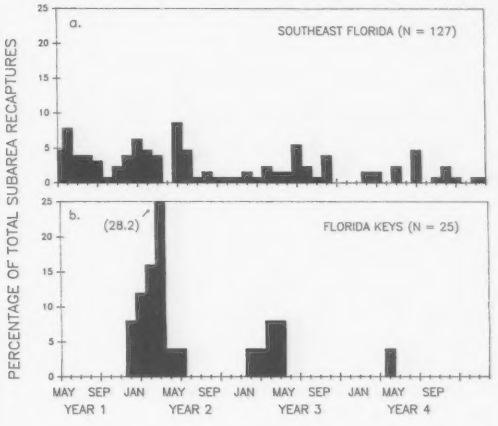


**Figure 5**

Monthly return percentage of king mackerel released from Jupiter region and recaptured in the (a) southeastern Florida (SEFL) and (b) Florida Keys (FK) subareas, using a continuous time-scale representative of relative time of freedom. Returns begin with May of year 1.

March, with numbers of recaptures steadily declining from Year 1 through Year 4 (Fig. 6b). A bimodal trend similar to that noted for fish released from the Ft. Pierce region (Fig. 4c) was also found for fish released from the Florida Keys region and recaptured in NEG waters (*N* 20; Fig. 6c). King mackerel returns were first reported during May and June from the NEG subarea. An increase in the frequency of tag returns from the NWG subarea (*N* 17) was then noted from June through August (Fig. 6d). King mackerel returned eastward to the NEG during August and September. These observations provide additional support for the possibility that king mackerel move annually through southeastern Florida and Gulf of Mexico waters.

## Spatial patterns of movement

King mackerel exhibited different patterns in relative magnitude and directionality as they moved away from their release regions. Of fish recaptured from releases from the South Carolina region, 54.3% (*N* 25) moved more than 100 km. None of these fish were reported farther north (Atlantic-ward) than North Carolina (450 km), whereas 78.6% of those moving Gulf-ward moved at least 650 km to southeastern Florida waters (Fig. 7a). There was no significant difference ($\chi^2$ 0.36, $0.50<P<0.75$) in the king mackerels' direction of movement away from the South Carolina region: 44.0% (*N* 11) moved Atlantic-ward and 56.0% (*N* 14) moved Gulf-ward.

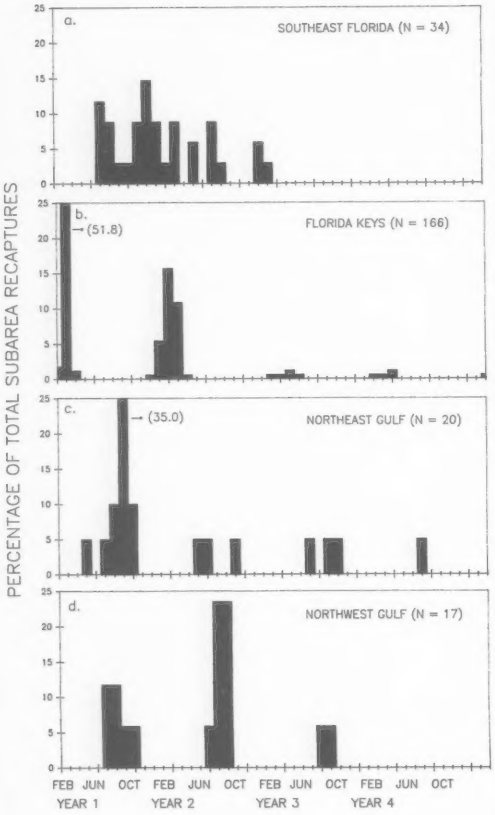
a.
SOUTHEAST FLORIDA (N = 34)
b.
FLORIDA KEYS (N = 166)
→ (51.8)
c.
NORTHEAST GULF (N = 20)
→ (35.0)
d.
NORTHWEST GULF (N = 17)
PERCENTAGE OF TOTAL SUBAREA RECAPTURES
FEB JUN OCT FEB JUN OCT FEB JUN OCT FEB JUN OCT
YEAR 1 YEAR 2 YEAR 3 YEAR 4

**Figure 6**

Monthly return percentage of king mackerel released from Florida Keys region and recaptured in the (a) southeastern Florida (SEFL), (b) Florida Keys (FK), (c) northeastern Gulf (NEG), and (d) northwestern Gulf (NWG) subareas, using a continuous time-scale representative of relative time of freedom. Returns begin with February of year 1.

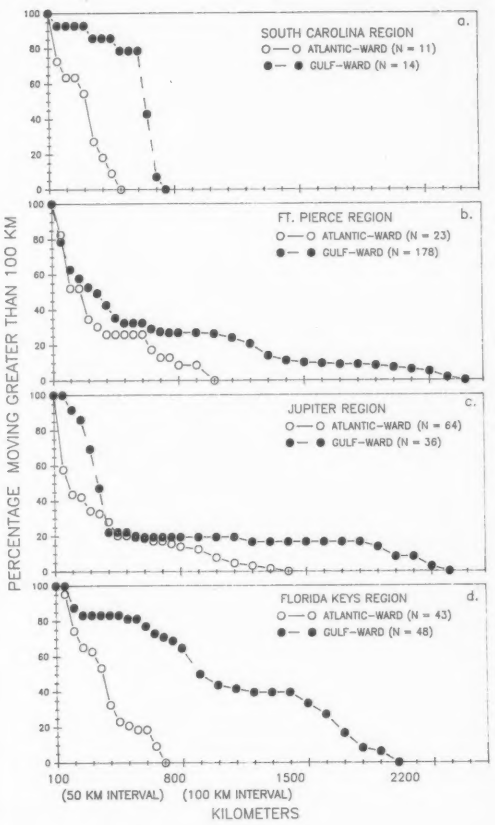
a.
SOUTH CAROLINA REGION
O— O ATLANTIC-WARD (N = 11)
●— ● GULF-WARD (N = 14)
b.
FT. PIERCE REGION
O— O ATLANTIC-WARD (N = 23)
●— ● GULF-WARD (N = 178)
c.
JUPITER REGION
O— O ATLANTIC-WARD (N = 64)
●— ● GULF-WARD (N = 36)
d.
FLORIDA KEYS REGION
O— O ATLANTIC-WARD (N = 43)
●— ● GULF-WARD (N = 48)
PERCENTAGE MOVING GREATER THAN 100 KM
100 800 1500 2200
(50 KM INTERVAL) (100 KM INTERVAL)
KILOMETERS

**Figure 7**

Relative movement of tagged king mackerel away from the four tagging regions of (a) South Carolina, (b) Ft. Pierce, (c) Jupiter, and (d) the Florida Keys, as a percentage of fish moving at least 100 km. The direction component is given by Atlantic-ward or Gulf-ward movement (see text for definitions).

A total of 37.0% (*N* 201) of the king mackerel recaptured from fish released from the Ft. Pierce region moved more than 100 km, with fish recaptured as far as 1000 km Atlantic-ward off North Carolina (Fig. 7b); fish moving Gulf-ward were recaptured as far away as Texas and Mexico (up to 2400 km). Within 800 km of the release site, the relative magnitude of movement away from the Ft. Pierce release region was similar for king mackerel with Gulf-ward affinity and those with Atlantic-ward affinity; however, a significantly greater number of fish ($\chi^2$ 119.53, $P<0.005$) moved Gulf-ward (88.6%; *N* 178). A similar trend in the relative magnitude of movement was noted for fish released from the Jupiter region; 48.3% (*N* 100) moved more than 100 km. A significantly higher percentage of these fish ($\chi^2$ 7.84, $P<0.01$) moved Atlantic-ward (64.0%; *N* 64; Fig. 7c). For fish moving more than 100 km (*N* 91), those tagged in the Florida Keys region moved farther from their release site into Gulf waters than did those fish moving Atlantic-ward (Fig. 7d). However, king mackerel released in the Florida Keys region did not show a significant difference in their relative direction of movement ($\chi^2$ 0.27, $0.50<P<0.75$): 47.3% (*N* 43) moved Atlantic-ward, 52.7% (*N* 48) moved Gulf-ward.

The number of days-at-large was significantly related to the distance that a fish traveled after release (Y-intercept 130.609, slope 0.072, *r* 0.122, df 1, 1148,

*F* 17.382). Several fish moved remarkable distances over short periods of time. For example, one fish released from Jupiter, Florida, traveled 2250km in 77 days before being recaptured off the southern Texas coast.

## King mackerel stocks in the southeastern United States

The percentages of king mackerel released as either Atlantic or Gulf stock and classified (using the posterior probability of the discriminant function analysis) into the same stock based on time and place of recapture are given in Table 2. The chi-square value for the test of homogeneity of the within-group covariance was significant ($\chi^2$ 41.89, df 6); therefore, the within-covariance matrices were used in this analysis. A total of 66.81% of king mackerel released as Atlantic stock was classified as the same stock upon recapture; therefore, this group was given a 66.81% affinity index value (Table 2). A 76.07% affinity index value was found for the Gulf of Mexico king mackerel stock. The percentage of classification for recaptured king mackerel in the five substocks is given in Table 3, again using the within-covariance matrices in the discriminant function ($\chi^2$ 245.87, df 24). All fish released in the SE U.S. Atlantic coast substock area were recaptured within the temporal and spatial definition of the Atlantic stock; i.e., they were all classified with either the SE U.S. Atlantic coast or southern Florida summer substocks (Table 3). Therefore, the SE U.S. Atlantic coast substock was given a 100% affinity value for the Atlantic stock. Southern Florida summer substock returns were similarly examined; 4.23% were classified with the SE U.S. Atlantic coast substock, and 53.97% were classified with the southern Florida summer substock, which yielded a 58.20% affinity index value. The combined Gulf substock had a 100% affinity-index value for the Gulf stock based on returns from the Florida Keys winter substock (9.09%) and from the Gulf waters (90.91%). The affinity-index value of the Florida Keys winter substock was 90.00% (Table 3), although some fish released in this area were classified in each of the five substock areas. King mackerel

**Table 2**
Posterior probability values for membership in either the Gulf or Atlantic stocks of king mackerel. Numbers of recaptured fish in parentheses.

| | Percentage classified into stock | | |
|---|---|---|---|
| Stock | Atlantic | Gulf | Affinity index |
| Atlantic | 66.81 (151) | 33.19 (75) | 66.81 |
| Gulf | 23.93 (162) | 76.07 (515) | 76.07 |

**Table 3**
Posterior probability values for membership in the five substocks of king mackerel. Numbers of recaptured fish in parentheses.

| | Percentage classified into stock | | | | | |
|---|---|---|---|---|---|---|
| | Atlantic | | Gulf | | | |
| Substock | SE U.S. Atlantic coast | South Florida, summer | Southeast Florida, winter | Florida Keys, winter | Gulf combined | Affinity of index |
| **Atlantic** | | | | | | |
| SE U.S. Atlantic coast | 91.89 (34) | 8.11 (3) | 0.00 (0) | 0.00 (0) | 0.00 (0) | 100.00 |
| South Florida, summer | 4.23 (8) | 53.97 (102) | 10.58 (20) | 31.22 (59) | 0.00 (0) | 58.20 |
| **Gulf** | | | | | | |
| Southeast Florida, winter | 5.58 (26) | 23.82 (111) | 14.81 (69) | 55.36 (258) | 0.43 (2) | 70.60 |
| Florida Keys, winter | 2.00 (4) | 8.00 (16) | 5.50 (11) | 80.50 (161) | 4.00 (8) | 90.00 |
| Gulf combined | 0.00 (0) | 0.00 (0) | 0.00 (0) | 9.09 (1) | 90.91 (10) | 100.00 |

released as southeastern Florida winter substock were also classified into all substocks, yielding a 70.60% affinity-index value (combined Gulf, 0.43%; Florida Keys winter, 55.36%; and southeastern Florida winter, 14.81%).

## Discussion

Two movement patterns were identified from our tagging study. King mackerel released in association with the Gulf of Mexico waters were found during winter months along the Florida Keys and along the southeastern Florida coast as far north as Cape Canaveral. By spring, these fish traveled along the western Florida coast toward northeastern Gulf waters, continuing westward during the summer. These king mackerel returned toward northwestern Florida in late-summer and early-fall, and then headed back to southern Florida waters by winter. Based on the recapture of fish from the same locations during roughly the same times of year over several consecutive years (e.g., Fig. 4a–d), we conclude that a periodic (annual) migratory behavior exists. The regularity of king mackerel movements through Gulf of Mexico waters was also noted during other tagging studies (Sutherland and Fable 1980, Fable 1988).

Trends of the catch-per-unit-effort (CPUE) for king mackerel from charterboat catches, reported by Trent et al. (1987), also support our conclusions. During 1983, 1984, and 1985, CPUE values of king mackerel generally increased along the northern Florida coast during late-May and June, followed by a peak in CPUE along the Alabama, Mississippi, and Texas coastlines. Another increase in CPUE was noted in Alabama during late-July and August, followed by a peak in northwestern Florida during late-August or early-September. Only winter peaks were noted in southern Florida, whereas no CPUE pattern was established for southeastern Florida. The lack of a consistent peak in this region as determined by tag returns from southeastern Florida may be evidence for a resident (i.e., nonmigratory) population. Fable et al. (1987) noted winter resident population of large king mackerel (>800 mm FL) in the northwestern Gulf of Mexico. We found no size-component associated with tagged fish either staying or leaving southeastern Florida waters ($\chi^2$ 8.19, $P>0.975$, df 18), based on length-frequency distributions of recaptured fish (50-mm FL interval, 400–1300 mm).

Movement of king mackerel along the Atlantic coast was not as clearly defined. Fish traveled south from South Carolina waters during the spring and summer, distributing themselves along the south Atlantic coast as far as the eastern and southwestern coasts of southern Florida, and then returned northward in late-summer and early-fall. Trent et al. (1987) noted an increase in CPUE from charterboat catches from North Carolina during April and again during October and November. Progressive increases in CPUE were noted in South Carolina during May and later during August and September; peaks were noted in Georgia and northeastern Florida during late-May (after South Carolina peaks) and again during August (before South Carolina peaks).

Spring and summer movements of king mackerel may reflect migrations to their respective spawning areas. After spawning, they return to wintering areas in the fall. Ichthyoplankton collections indicate that king mackerel from the Atlantic coast spawn from April through October, with a peak during September (Collins and Stender 1987). Gulf of Mexico larvae collections and reproduction indices suggest a similar spawning season for the Gulf stock (Wollam 1970, Dwinell and Futch 1973, McEachran et al. 1980, Finucane et al. 1986).

King mackerel movement patterns, as determined from temporal and spatial variability in tag returns, must be viewed in relative and descriptive terms rather than in absolute rates of movement. The percentages of returns varied from 5.69% (South Carolina region) to 9.68% (Florida Keys region), but when numbers of recaptures were compartmentalized by subareas, these values were subsequently reduced. This reduction was magnified as distance from release site increased. Lower percentage of returns may be a function of actual proportion of fish moving away from location of release but may also reflect relative changes in effort and availability over time, or may be indicative of a "dilution" of tagged fish by king mackerel from other locations (e.g., with a resident population in the northwestern Gulf of Mexico). Combinations of these factors, as well as other environmental and biological parameters, are probably interacting, but are beyond the resolution ability of our database. However, we feel the observed trends, together with published information previously discussed, are strong enough to support our conclusions of king mackerel movement through SE U.S. waters.

Distance from the 'transition zone' along the southern Florida coast (Fig. 1, shaded area) was related to the affinity-index values calculated for each substock. Both the South Atlantic and combined Gulf substocks, located outside this transition area, had 100% classification (affinity) values with the appropriate Atlantic or Gulf stock. The Florida Keys winter substock, located in the southwest edge of this transition area, was closely tied to the Gulf stock (90.00% affinity). King mackerel released in southeastern Florida had the lowest affinity values (Table 3). Winter releases from

the Ft. Pierce region (southeastern Florida winter substock), which would be included within the scope of the Gulf stock, were mistakenly classified 29.40% of the time with Atlantic stock waters. Most of these misclassifications were temporal in nature, the recaptures having been taken during summer months from southeastern Florida. The low affinity-index value for summer-month releases from Jupiter (southern Florida summer substock) is a result of fish being recaptured within either the Florida Keys winter substock (31.22%) or the southeastern Florida winter substock (10.58%) areas, yielding a total misclassification of 41.80% of Atlantic stock with Gulf stock waters.

Southeastern Florida waters are important to both Atlantic and Gulf stocks. Both stocks occupy this area during some part of the year; the observed seasonal overlap may range from 29.40% to 41.80% (Table 3) based on percent misclassification. The management problems of a mixed-stock fishery system are recognized (Hilborn 1985, Sinclair et al. 1985). For effective management an accurate distinction between stocks is vital (Misra 1985), yet genetic differentiation using electrophoretic variation has not yielded any differences between Gulf and Atlantic stocks of king mackerel (May 1983, Johnson 1988). An alternative management strategy, therefore, may be to designate the area between the Collier/Monroe line on the southwestern Florida coast and the Florida/Georgia line on the Atlantic coast as a mixing zone, to be managed with the most conservative measures available (i.e., Gulf or Atlantic stock) to ensure adequate stock protection.

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# Effect of Tag Anchor Location on Retention/Survival through Molt in Male Snow Crabs *Chionoecetes opilio*

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**Abstract.**–A laboratory study showed that when small male snow crabs are tagged with the anchor of a t-bar tag inserted into the dorsal musculature, tag retention and survival through the first molt are excellent; when the tag anchor is situated in the basal leg musculature, animals die while molting. When recaptures were obtained from larger, field-tagged animals, it was noted that some animals which had molted had been tagged in the leg musculature. Dissections were performed on 43 animals which molted and 89 animals which did not molt to determine tag anchor placement. Four general locations were noted: dorsal musculature, basal leg musculature, loose in the body cavity, and attached internally to carapace. Relative tag retention/survival associated with molting was estimated for the different tag anchor locations by comparing the proportions of tags in each location among animals which molted and among those which did not. Animals with anchors in the leg musculature appeared to survive and retain the tag through a molt as well as those tagged in the dorsal musculature and those with the tag attached to the inside of the carapace. Animals with anchors loose in the body cavity appeared to have worse tag retention/survival than those tagged in the dorsal musculature. The hypothesis that tag placement does not affect retention/survival through molt was tested by fitting hierarchical loglinear models and testing for a significant interaction between molt status (i.e., did or did not molt) and tag anchor location. No statistically significant effect was found, but it still seems prudent to try to place tag anchors into the dorsal musculature.

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A tagging study was initiated in Conception Bay, Newfoundland, Canada, to determine the growth in size of male snow crabs *Chionoecetes opilio* at the time of molting. The t-bar tag (Floy Tag Mfg. Co., Inc., Seattle, WA 98105) was selected because preliminary studies had shown that the tag can be retained through a molt (McBride 1982, Taylor 1982). Early tag return rates were lower than expected, so a study was initiated to evaluate the performance of the tag when applied to animals held in captivity (Hurley et al. 1990). The laboratory study, conducted on animals ranging in size from 60 to 83 mm CW (carapace width), demonstrated that survival and retention of tags through a molt was excellent, provided the tag anchor was inserted into the dorsal musculature (Fig. 1). However, when the tag anchor was inserted into the basal leg musculature, the animals died during the molt. Tissue necrosis associated with *Pseudomonas* sp. bacteria was frequently noted around the tag anchor regardless of where it was located in the body.

For the Conception Bay study, an effort was made to carefully insert the tag anchors into the dorsal musculature. It was therefore surprising when some animals that had molted were recaptured with the anchor in the basal leg musculature. Also, some crabs had tags with the anchor loose in the body cavity, while in others it was attached to the carapace. Since the animals examined in the field study were larger (82–120 mm CW at tagging) than the ones used in the laboratory study, it was hypothesized that placement of the tag anchor may not be as critical for large animals as for smaller ones.

In this paper, we present the results of dissecting 132 recaptured animals to determine location of the tag anchor within the body. We develop analytical procedures to estimate the relative rate of tag retention and survival at the time of molting for different anchor locations. We test the hypothesis that retention/survival is the same for all locations using hierarchical loglinear models.

## Materials and methods

Male snow crabs were tagged in Conception Bay during 1983 and 1984 using methods described by Hurley et al. (1990) and Taylor and Hoenig (1990). The t-bar tag consists of a vinyl anchor 8 mm long, 1.2 mm in diameter, attached perpendicularly to a 25 mm-long shaft, 0.5 mm in diameter, which in turn connects to a 50-mm length of Number 20 vinyl tubing printed with identificaion information. Tags were inserted through the posterior ecdysial suture (epimeral line) which was made visible by applying gentle upward pressure to the carapace. The location of tag insertion was on the right side of the body 2–6 mm from the coxopodite of the last walking leg (Fig. 1). Before releasing the crab, the end of the tag

was given a gentle tug. If the tag appeared loose, it was removed and the animal was discarded.

Recaptured animals were obtained from commercial fishermen and stored in a freezer. Animals were then thawed and dissected in order to determine the location within the animals of the tag anchor. The carapace was cut diagonally on either side of the protruding tag by inserting the lower blade of a pair of scissors into the epimeral line. The forward portion of the triangular piece of cut carapace was then lifted to uncover the end of the tag. Tags were classified as being in one of four positions (Table 1): (1) anchor lodged in the dorsal musculature; (2) anchor loose in the body cavity, e.g, nestled against the hepatopancreas; (3) anchor lodged in the soft, newly forming carapace under the hard carapace, or attached to the underside of the hard carapace; and (4) anchor lodged in the basal leg musculature. The extent of any necrotic tissue around the anchor was also noted (Table 2).

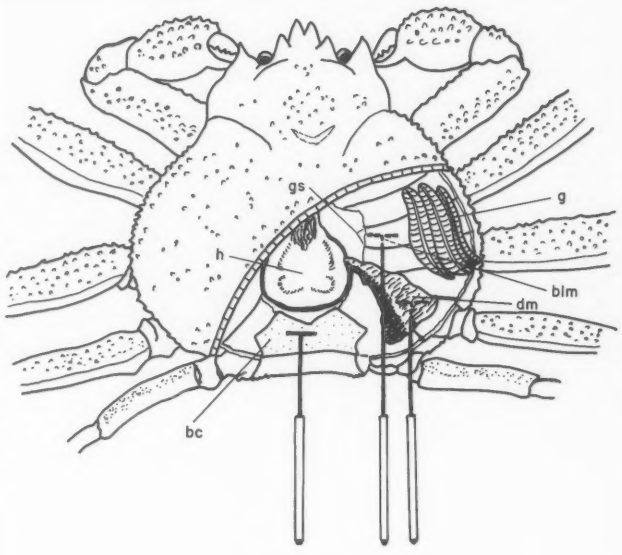


**Figure 1**
Drawing of a male snow crab with part of the dorsal carapace removed to show tagging locations referred to in text: bc = body cavity, blm = basal leg musculature, dm = dorsal musculature, g = gills, gs = gill septum, h = heart.

## Analysis of recapture data

The logic of our analysis is as follows. We don't know the proportion of animals with the tag anchor placed in each of the four locations, and we don't know the magnitude of any initial tag loss or mortality immediately (within one month) following release of the tagged animals. However, those recaptured animals at liberty for more than one month which did not molt provide an estimate of the proportions of animals with tag anchors in each location prior to molting. Similarly, the recaptured animals which did molt provide an estimate of the proportions after molting. Consequently, differences in the proportions reflect different tag retention and/or survival.

**Table 1**
Recapture data for male *Chionoecetes opilio* tagged in Conception Bay, Newfoundland, given by year of tagging, molt status (molted vs. did not molt), location of tag anchor within the body, and data pooled over the 2-year period.

| Recapture of animals tagged in: | Molt status | Tag locations | | | |
|---|---|---|---|---|---|
| | | dorsal musculature | loose in body | in shell | leg musculature |
| 1983 | did not molt | 7 | 2 | 8 | 7 |
| | molted | 4 | 1 | 4 | 3 |
| 1984 | did not molt | 29 | 14 | 11 | 11 |
| | molted | 16 | 1 | 6 | 8 |
| Years combined | did not molt | 36 | 16 | 19 | 18 |
| | molted | 20 | 2 | 10 | 11 |

This analysis requires two assumptions: (1) tags in all of the tagging locations affect the timing of molting in the same way (if at all); (2) differential mortality and tag loss among tagging locations is zero both prior to and subsequent to molting (with the possible exception of the period immediately after tagging and release of animals). A number of studies have shown that molting can be a critical period for tag-induced mortality and tag shedding (Restrepo and Hoenig 1988, Hurley et al. 1990). Hence, it is reasonable to presume that if animals survive the first month at liberty with their tag intact, then they are likely to remain viable until the time of molting.

Consider the recapture data for 1984 in Table 1. The relative abundance of animals with tag anchors loose in the body cavity and in the dorsal musculature, among animals which did not molt, is 14:29 or 0.48:1. Among animals which molted, the relative abundance is 1:16

**Table 2**

Incidence of necrosis around the tag anchor in male *Chionoecetes opilio* tagged in Conception Bay, Newfoundland, with t-bar tags.

| | Tagging location | | | |
|---|---|---|---|---|
| | Dorsal muscle | Body cavity | Shell | Leg muscle |
| Number with necrosis | 11 | 4 | 7 | 7 |
| Number without necrosis | 45 | 14 | 22 | 25 |
| % necrotic | 20 | 22 | 24 | 22 |

or 0.06:1. Hence animals with anchors loose in the body cavity appear to have become less abundant relative to those tagged in the dorsal musculature, and this suggests lower tag retention and/or lower survival for animals with anchors loose in the body cavity. In fact, the relative retention/survival rate can be estimated from the 1984 data as

$$\alpha = \text{relative retention/survival (loose:dorsal)}$$

$$= \frac{\frac{1}{16}}{\frac{14}{29}} = \frac{1 \cdot 29}{16 \cdot 14} = 0.13.$$

The estimator $\alpha$ is the cross-product ratio frequently used in survival analysis (Fienberg 1980).

If all data were collected from animals tagged in the same year, then it would be a simple matter to use a $\chi^2$ test to test the null hypothesis that the proportions in each location are the same for the two molt states (molted versus did not molt). However, animals were tagged in two separate years and there is at least a reasonably strong possibility that the tagging procedure varied between the years, e.g., due to developing tagging skill. This suggests that the interaction terms involving year may be significant. If interaction terms are ignored and the data from different years are pooled, then associations between variables (i.e., between molt status and tagging location) can be distorted and the apparent direction of the association can even reverse (see Fienberg 1980, chap. 3). An analysis which explicitly accounts for this possibility can be conducted using hierarchial loglinear models.

The 16 counts in Table 1 for individual years 1983 and 1984 can be envisioned as comprising a $2 \times 2 \times 4$ contingency table with main effects (categorizations) due to year of tagging (Yr), molt status (Molt), and location of tag within the body (Loc). There are nine loglinear models that can be fitted to these data (Table 3) ranging from the model of complete independence through seven models of partial dependence to the completely saturated model (see Fienberg 1980 for a discussion). The contingency table can be collapsed over the year variable if one (or both) of the two-factor interactions involving year is not significant. The hypothesis that tagging location has no influence on retention/survival through molt can be rejected if it is necessary to have an interaction between location and molt status (Loc*Molt) to have a good fit to the data.

Even the simplest model of main effects only (model 1) is not rejected by the likelihood ratio test ($P = 0.2067$, Table 3). It is still of interest to explore how strong the evidence may be that location of the tag affects survival/retention through the molt. We will therefore examine the following four models in more detail.

model 1:
Count = [Molt] [Yr] [Loc]
model 3:
Count = [Molt] [Yr] [Loc] [Yr]*[Loc]
model 4:
Count = [Molt] [Yr] [Loc] [Molt]*[Loc]
model 5:
Count = [Molt] [Yr] [Loc] [Molt]*[Loc] [Yr]*[Loc]

**Table 3**

Loglinear model analysis of tagging count data in Table 1. C is the predicted count, [Yr] represents year of tagging, [Molt] represents molt status, and [Loc] represents location of the tag anchor within the body. Asterisk (*) indicates an interaction between variables. To make the notation more compact, only the highest-order interactions are given for each variable. For example, the model C = [Loc] [Yr]*[Molt] represents main effects for location, year, and molt, plus the interaction between year and molt. The order of presentation of the variables has no significance in the model notation.

| Model | Likelihood ($\chi^2$) | df | $P$ |
|---|---|---|---|
| 1) C = [Yr] [Molt] [Loc] | 13.31 | 10 | 0.2067 |
| 2) C = [Yr]*[Molt] [Loc] | 13.30 | 9 | 0.1495 |
| 3) C = [Molt] [Yr]*[Loc] | 7.03 | 7 | 0.4262 |
| 4) C = [Yr] [Molt]*[Loc] | 8.11 | 7 | 0.3233 |
| 5) C = [Yr]*[Loc] [Molt]*[Loc] | 1.82 | 4 | 0.7688 |
| 6) C = [Yr]*[Molt] [Loc]*[Molt] | 9.09 | 6 | 0.2313 |
| 7) C = [Molt]*[Yr] [Loc]*[Yr] | 7.01 | 6 | 0.3196 |
| 8) C = [Molt]*[Yr] [Loc]*[Yr] [Molt]*[Loc] | 1.81 | 3 | 0.6120 |
| 9) C = [Yr]*[Molt]*[Loc] | 0 | 0 | 1.0000 |

The above model descriptions are a common way of representing loglinear models. Model 1 indicates that the logarithm of the count in any cell can be predicted as the sum of the main effects for molt status, year of tagging, and location, i.e., these factors act independently. Model 3 is the same as model 1 except that an interaction term (or dependency) between year of tagging and location of anchor is also needed to predict the counts. Model 4 has a similar interpretation but the logarithm of the count depends on an interaction between anchor location and molt status. Model 5 includes the interaction between year and location and between molt status and location. Thus, models 1 and 3 imply no differential survival/tag retention among tagging locations, whereas models 4 and 5 imply that tagging location has an effect on the probability of surviving a molt with the tag still in place.

The difference between models 1 and 3 is that model 3 implies that the proportions of animals tagged in each location varied between the two years while model 1 implies the same proportions occurred in both years. If year has no effect on location (i.e., the interaction between year and location is unimportant), then a test of the effect of location on survival/retention through molt can be achieved by comparing models 1 and 4. But, if the proportions tagged in each location varied among the years, then the comparison that isolates the effect of tagging location on survival/retention through molt is the comparison of models 3 and 5.

The choice between two nested models can be made on the basis of a likelihood ratio test by subtracting the log-likelihoods and referring to a $\chi^2$ table with degrees of freedom equal to the difference in degrees of freedom for the two models. The computed test statistic for comparing models 1 and 3 is

$$\chi^2_{comp} = 13.31 - 7.03 = 6.28, \quad df = 10 - 7 = 3$$

and the resulting $P$-value is 0.099. We fail to reject model 1 in favor of model 3 at the 5% level and conclude that the evidence is not strong enough to conclude that the proportions tagged in each body location varied by year. However, the test results could be considered marginally or nearly significant.

The hypothesis of interest is whether the tagging location affects the survival/retention through molt. This can be accomplished by comparing models 1 and 4,

$$\chi^2_{comp} = 13.31 - 8.11 = 5.20, \quad df = 10 - 7 = 3,$$

for which the $P$-value is 0.1577. Alternatively, we can compare models 3 and 5 and obtain virtually the same results. Thus, the statistical evidence is not strong enough to conclude that location affects survival/retention through molt at the customary 5% level. However, in light of the small sample sizes and possible low power of the test, the results provide some evidence, albeit weak, that location may be important.

Since at least one two-factor interaction involving year is not significant in each of the models we considered, one can validly collapse the three-dimensional table over year to obtain a $2 \times 4$ table. The estimated relative retention/survival rates, $\alpha$, can be computed from the pooled data (Table 1). Relative to animals tagged in the dorsal musculature, the tag retention/survival of animals with tag anchors loose in the body cavity, embedded in shell, and in the dorsal leg musculature are estimated to be 0.23, 0.95, and 1.10, respectively.

Although 18% of the dissected animals had some blackening around the anchor of the tag, only 2 animals (1.5%) had extensive areas of necrosis. All animals had been at liberty for at least a year. The proportion of animals with necrotic tissue did not appear to vary much among the different tagging locations (Table 2).

## Discussion

Although the laboratory study indicated that tagged animals die at the time of molting if the tag anchor lodges in the basal leg musculature, there was no evidence of this in the field data. We hypothesize that this is because the field-tagged animals were larger than the laboratory animals, and larger animals may tolerate a tag in the leg musculature better than smaller animals. If relative retention/survival due to anchor location depends on size of the animals, then size category should be considered as another variable in the analysis. However, in our field study only animals in a narrow range of sizes (82–120 mm CW at tagging) were examined so that there seems little point in dividing the limited number of recaptures into size classes.

Since the field data indicate that having the end of the tag loose in the body cavity reduces the chances of recovering the animal with tag intact ($\alpha$ 0.23), and the laboratory data indicate that tagging in the basal leg musculature reduces recoveries, it seems prudent to try to insert the tag anchor into the dorsal musculature. Our lack of statistically significant results does not imply that tagging location is not a significant biological factor in determining the success of a tagging program. Rather, it may simply indicate that our sample sizes were inadequate to obtain strong evidence of the importance of location. We recommend that, prior to initiating a field tagging program, a few trial animals be sacrificed to determine how consistently the tag anchor is being placed into the targeted dorsal musculature.

The loglinear model approach we used is quite general and allows any number of covariates (such as size at the time of tagging) to be properly accounted for. For those who prefer a regression approach to data analysis, the same analyses can be cast as logit models (see Fienberg 1980, chap. 6).

The laboratory study by Hurley et al. (1990) suggested that tag insertion frequently results in extensive necrosis of the tissue and carapace around the anchor. This was not seen in the field data. We speculate that the decreased levels of necrosis in the field-tagged animals may be due to the lower water temperatures in Conception Bay ($-1.2$ to $-0.5$°C in the Bay versus 4–6°C in the laboratory study).

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# Seasonal and Annual Variability in the Diet of California Sea Lions *Zalophus californianus* at San Nicolas Island, California, 1981-86

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California sea lions haul out and breed on islands along the Pacific coasts of southern and Baja California and in the Gulf of California. About half of all births occur in southern California waters (Fig. 1), principally at San Miguel and San Nicolas Islands (Stewart et al. In press). Some studies have shown that diet varies geographically, perhaps influenced by seasonal variability of various prey (Fiscus and Baines 1966, Ainley et al. 1982, Everitt et al. 1981, Hawes 1983, Antonelis et al. 1984, Aurioles et al. 1984, Antonelis et al. 1990, Lowry et al. 1990). Here we describe seasonal and annual variability in the diet of California sea lions that hauled out at San Nicolas Island from 1981 through 1986.

## Methods

We collected sea lion scats every one or two months at several rookeries and hauling grounds at San Nicolas Island (Fig. 1). Scats were washed through nested sieves (mesh sizes of 2.8 mm, 1.5 mm, and 0.71 mm) to recover hard parts such as fish otoliths, cephalopod beaks (i.e., mandibles), shark teeth, and invertebrate exoskeletal fragments. We identified prey species by comparing those remains with museum and personal voucher collections.

The frequency of occurrence (FO) of each prey taxon was calculated as the proportion of scats in each sample that contained at least one hard part from a prey taxon. We pooled monthly samples into four groups: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). We tested the null hypotheses that frequencies of occurrence of the most common prey (those that occurred in 5% or more of all scats) did not differ among seasons nor among years using a two-way analysis of variance (Program 7D of BMDP-87; Dixon 1987); we excluded data for 1981 from this analysis because we lacked data for some seasons. We tested the null hypothesis that dietary diversity did not differ among seasons or among years using multiway contingency table analysis (Program 4F of BMDP-88; Dixon 1988).

## Results

We examined 1232 scats from summer 1981 through autumn 1986; 1085 of those contained identifiable prey hard parts (Table 1). We identified 32 prey taxa to species and 6 to genus, but only two genera of cephalopods and five of fish occurred in 5% or more of the scats. Therefore, we confined our analyses of seasonal and annual variability in diet to the latter 7 taxa. Northern anchovy *Engraulis mordax* was the most common prey, occurring in about half (50.6%) of all scats; Pacific whiting *Merluccius productus*, jack mackerel *Trachurus symmetricus*, rockfish *Sebastes* spp., and market squid *Loligo opalescens* each occurred in about 22–30% of scats (Table 2).

We are limited in our generalizations about seasonal trends in the frequencies of occurrence of prey species because of strong seasonal-annual interactions (ANOVA, $P < 0.05$). There are, however, some differences apparent among some seasons and years (Fig. 2). Northern anchovy was eaten more often in winter than in other seasons in 1982, 1983, and 1984, but not in 1985 or 1986; anchovy was present in more than 60% of scats each season in 1986. Furthermore, anchovy occurred in scats more often from 1984 through 1986 than in earlier years. Pacific whiting was eaten frequently from summer 1981 through spring 1982, and in spring

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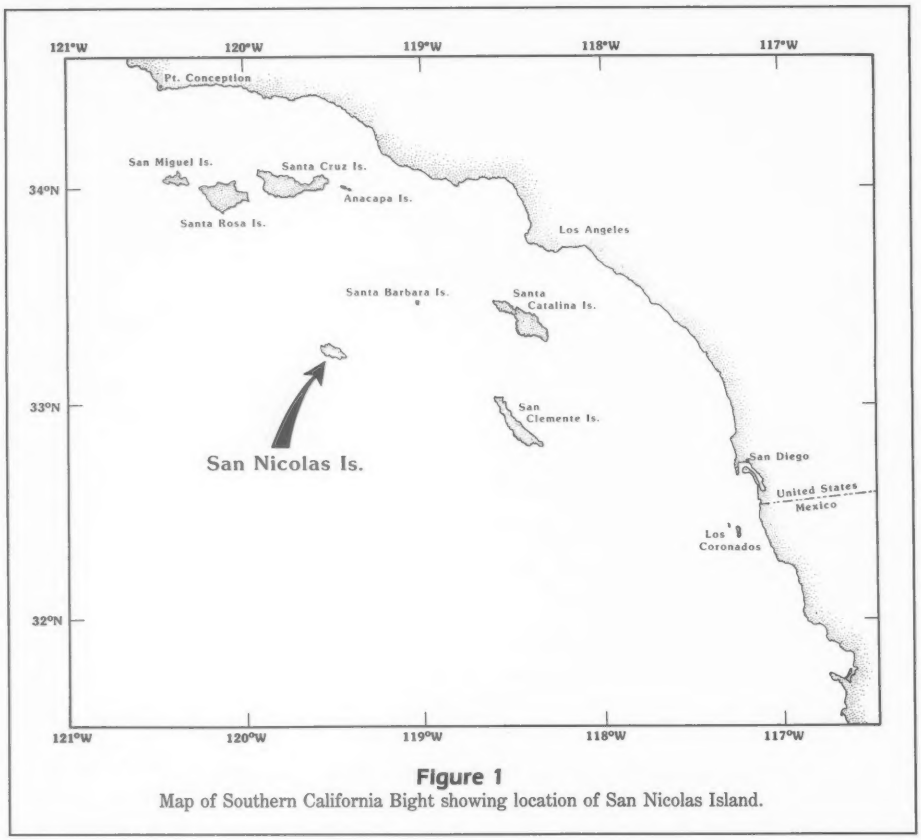


**Figure 1**
Map of Southern California Bight showing location of San Nicolas Island.

**Table 1**
Scat samples of *Zalophus californianus* collected at San Nicolas Island, California.

| Year | Winter | Spring | Summer | Autumn | Total |
|---|---|---|---|---|---|
| 1981 | 0 | 0 | 24 | 18 | 42 |
| 1982 | 12 | 15 | 68 | 13 | 108 |
| 1983 | 4 | 42 | 150 | 55 | 251 |
| 1984 | 75 | 35 | 107 | 93 | 310 |
| 1985 | 62 | 77 | 64 | 63 | 266 |
| 1986 | 35 | 24 | 80 | 116 | 255 |
| Total | 188 | 193 | 493 | 358 | 1232 |

1984 through spring 1985. Jack mackerel was found in scats more often in summer 1981 through autumn 1983 than after that period. Rockfish were commonly found in winter 1982, and spring 1984 through spring 1985. Market squid was more common in the diet prior to 1983 and its frequency of occurrence was higher in either autumn or winter, or both, each year except in 1984. Pelagic red crabs *Pleuroncodes planipes* appeared in scats in 1983, were frequently eaten through 1985, and then disappeared from the sea lions' diet. Pacific mackerel occurred frequently in summer and autumn 1982. *Octopus* spp. were eaten more often in spring 1984 than at any other time and appeared in the diet mostly in spring and summer of all years.

About 69% of all scats contained one or two prey taxa (Fig. 3). There were significant season-year interactions ($P<0.05$) for all years and seasons, but the number of prey taxa occurring in each scat was greatest from 1981 through 1984 and least in 1985 and 1986 (Fig. 3).

## Discussion

California sea lions forage in a number of different habitats and depth strata in the Gulf of California and along the North American Pacific coast from Baja California to British Columbia. The composition of the sea lions' diet varies geographically (Jameson and

**Table 2**

Prey found in scat samples ($n$) and frequency of occurrence (expressed in %) for prey found in 1085 California sea lion scats collected at San Nicolas Island, California, 1981–86.

| Prey | | | |
|---|---|---|---|
| Scientific name | Common name | $n$ | % |
| **Teleosts** | | | |
| *Engraulis mordax* | northern anchovy | 550 | 50.6 |
| *Merluccius productus* | Pacific whiting | 318 | 29.3 |
| *Trachurus symmetricus* | jack mackerel | 303 | 27.9 |
| *Sebastes* spp. | rockfish | 282 | 25.9 |
| *Scomber japonicus* | Pacific (chub) mackerel | 123 | 11.3 |
| *Chromis punctipinnis* | blacksmith | 22 | 1.9 |
| *Oxyjulis californica* | señorita | 15 | 1.3 |
| *Porichthys notatus* | plainfin midshipman | 5 | 0.4 |
| *Cololabis saira* | Pacific saury | 5 | 0.4 |
| *Icichthys lockingtoni* | medusafish | 5 | 0.4 |
| *Lycodes cortezianus* | bigfin eelpout | 4 | 0.3 |
| *Chilara taylori* | spotted cusk-eel | 3 | 0.2 |
| *Microstomus pacificus* | dover sole | 3 | 0.2 |
| *Citharichthys* spp. | sanddab | 3 | 0.2 |
| *Cymatogaster aggregata* | shiner surfperch | 3 | 0.2 |
| *Zalembius rosaceus* | pink seaperch | 3 | 0.2 |
| *Lyopsetta exilis* | slender sole | 2 | 0.2 |
| *Leuroglossus stilbius* | California smoothtongue | 2 | 0.1 |
| *Symbolophorus californiensis* | California lanternfish | 2 | 0.1 |
| *Sardinops sagax* | Pacific sardine | 2 | 0.1 |
| *Phanerodon furcatus* | white seaperch | 2 | 0.1 |
| *Zaniolepis* spp. | combfish | 2 | 0.1 |
| *Citharichthys sordidus* | Pacific sanddab | 2 | 0.1 |
| *Girella nigricans* | opaleye | 1 | 0.1 |
| *Medialuna californiensis* | halfmoon | 1 | 0.1 |
| *Argentina sialis* | Pacific argentine | 1 | 0.1 |
| *Stenobrachius leucopsarus* | northern lampfish | 1 | 0.1 |
| *Anoplopoma fimbria* | sablefish | 1 | 0.1 |
| *Icelinus tenuis* | spotfin sculpin | 1 | 0.1 |
| Unid. Myctophidae | lanternfish | 10 | 0.9 |
| Unid. Embiotocidae | surfperch | 3 | 0.2 |
| | unid. fishes | 72 | 6.6 |
| | unid. flatfish | 3 | 0.2 |
| **Elasmobranchs** | | | |
| *Prionace glauca* | blue shark | 1 | 0.1 |
| **Cephalopods** | | | |
| *Loligo opalescens* | market squid | 238 | 21.9 |
| *Octopus* spp. | octopus | 70 | 6.4 |
| *Onychoteuthis borealijaponicus* | squid | 52 | 4.7 |
| *Abraliopsis* spp. | squid | 24 | 2.2 |
| *Gonatus* spp. | squid | 18 | 1.6 |
| *Gonatopsis borealis* | squid | 13 | 1.1 |
| *Chiroteuthis calyx* | squid | 1 | 0.1 |
| Unid. Gonatidae | squid | 4 | 0.3 |
| | unid. cephalopod | 20 | 1.8 |
| **Crustaceans** | | | |
| *Pleuroncodes planipes* | pelagic red crab | 118 | 10.8 |
| | unid. crustacean fragments | 5 | 0.4 |
| **Algas** | | | |
| Unid. Algae | algae | 6 | 0.5 |

Kenyon 1977, Bowlby 1981, Everitt et al. 1981, Jones 1981, Bailey and Ainley 1982, Antonelis et al. 1984, Aurioles et al. 1984, Roffe and Mate 1984), but dietary diversity appears to be rather low in each location relative to the number of prey taxa consumed rangewide. Our studies of seasonal and annual variability in diet of sea lions at San Nicolas Island further support the classification of California sea lions as plastic specialists (Morse 1980). California sea lions exploit a few resources at a time, but prey composition of the diet is temporally dynamic; they capitalize on the more seasonally abundant and accessible schooling or aggregating prey.

The dietary occurrence of the sea lions' primary prey (northern anchovy, Pacific whiting, rockfish, jack mackerel, and market squid) appears to be related to the seasonal and annual occurrence of those prey species near San Nicolas Island. Market squid were eaten most often in autumn and winter in most years corresponding with the seasonal nearshore movements of spawning squid in this area (Bedford et al. 1983, Klingbeil 1986). Market squid were not commonly eaten by sea lions in 1983 and 1984, a time when squid were uncommon in the Southern California Bight (cf. Bedford et al. 1983; Klingbeil 1984, 1985, 1986; Grant 1987).

The presence of northern anchovy in the diet of sea lions seems to be related to the availability of anchovy near San Nicolas Island. Northern anchovy were uncommon near San Nicolas Island from 1982 through 1984, but were quite abundant in that area in 1985 and 1986 (Bindman 1986, Methot and Lo 1987). Sea lions consumed northern anchovy frequently in all seasons in 1985 and 1986, but substantially lower from 1981 through 1984, except during winter when anchovy were spawning and evidently nearer to San Nicolas Island than in other seasons.

The number of prey taxa eaten appears to be closely linked to the abundance and availability of northern anchovy. When anchovy were abundant near San Nicolas Island, sea lions evidently ate them in preference to other species. Both seasonal and annual patterns indicate that when the frequency of occurrence of anchovy in the diet is high, the number of prey species consumed is low. When northern anchovy are not available the breadth of the diet increased, with 3 to 4 other species being eaten.

Jack mackerel were displaced northward out of the Southern California Bight in 1984 when ocean surface currents changed and warm water associated with the 1982/83 El Niño-Southern Oscillation intruded into that area from Baja California (Mason 1989); the presence of jack mackerel in sea lion scats declined substantially then. Pelagic red crabs were transported into the Southern California Bight during this warm-water intrusion and they were frequently eaten by sea lions in 1983 and, to a lesser extent, through 1985 when they disappeared from their diet.

The dietary and behavioral flexibility of California sea lions in response to movements and availability of prey and to environmental perturbations (e.g., El Niño Southern Oscillation) may be one of the most important factors contributing to the consistent increase in their abundance during the past several decades. Relative to other locations, it appears that northern anchovy may be one of the most important prey of California sea lions near San Nicolas Island. This regional phenomenon is due to the proximity of San Nicolas Island to large spawning aggregations of northern anchovy compared with other locations where dietary studies of California sea lion have been made.

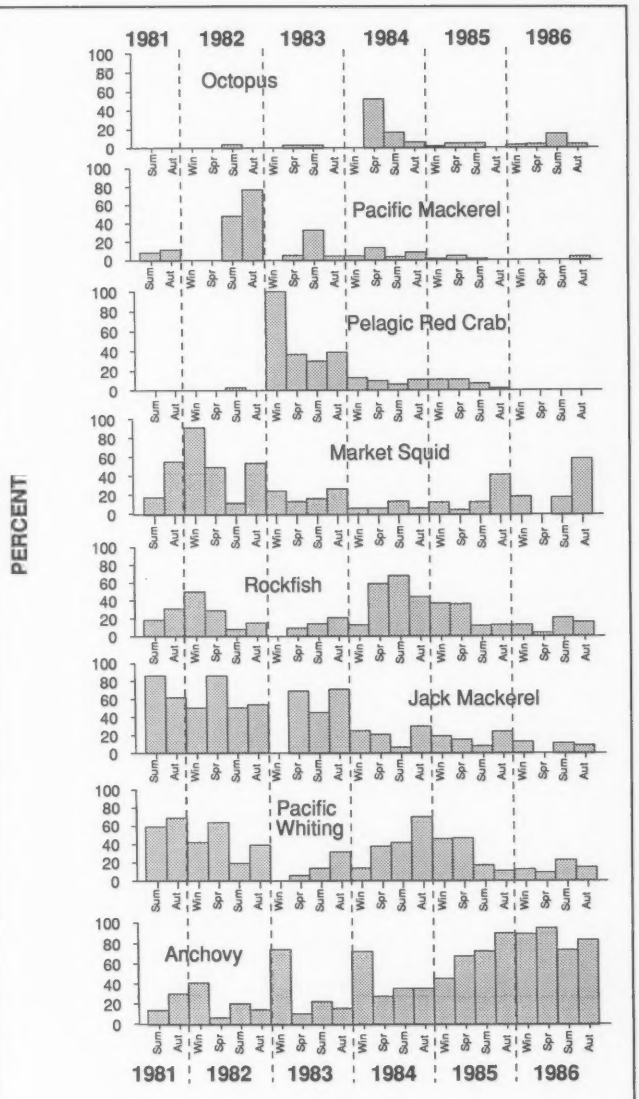


**Figure 2**
Seasonal frequency of occurrence (%) for eight prey taxa found in California sea lion scats collected at San Nicolas Island, California.

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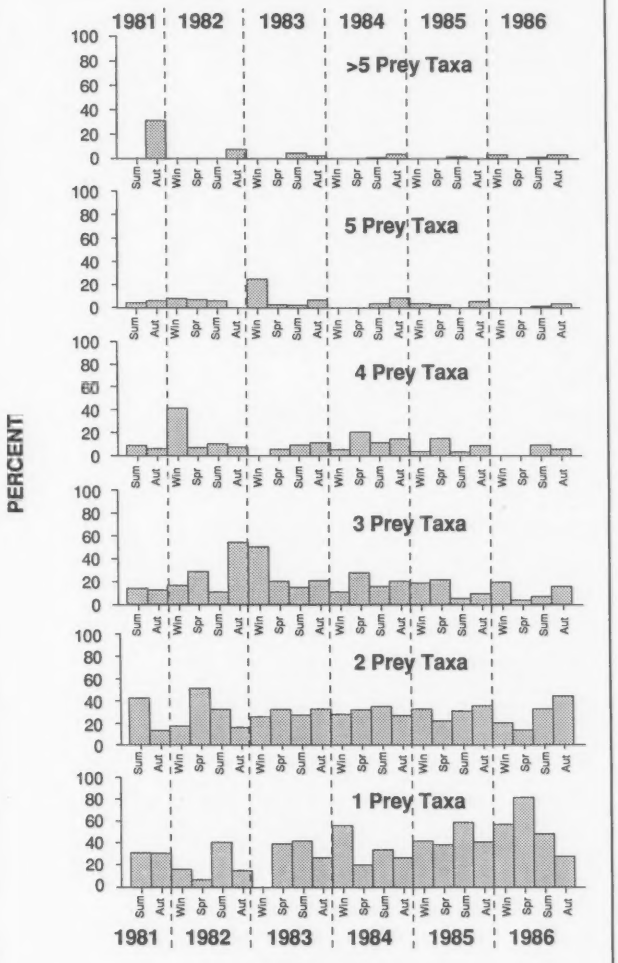


**Figure 3**

Frequency distributions of the numbers of prey taxa found in California sea lion scats collected at San Nicolas Island, California, summer 1981–autumn 1986.

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# Automated Enumeration by Computer Digitization of Age-0 Weakfish *Cynoscion regalis* Scale Circuli*

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There has been extensive use of daily otolith growth increments in age and growth studies of age-0 fishes (Campana and Neilson 1985). Recently, the daily ageing method has been extended to scales (Szedlmayer et al. In press). However, visually counting increments is tedious, time consuming, and subject to human error (Rice 1987). In an effort to automate the counting of increments or daily circuli in scales of age-0 juvenile weakfish *Cynoscion regalis*, a microcomputer-based system was used to digitize the video image of a scale, store the light intensities from a radial transect, and count circuli. Circuli were also counted visually to verify the accuracy of the software. Others have used microcomputer-based systems to aid in increment counting (Tzeng and Yu 1988, Thorrold and Williams 1989, Karakiri et al. 1989), but to our knowledge the present algorithm is the first method that completely automates increment counting with a high degree of accuracy.

## Materials and methods

Age-0 juvenile weakfish were collected from the York River, Virginia (for further collection methods, see Szedlmayer et al. 1990). Fish, 50–140 mm standard length ($n$ = 45), were anesthetized with tricane methanol sulfate (50 mg MS-222/L seawater), and scales removed from just below the midbody lateral line curve. The scales were placed on a glass slide in water and cleaned with a paint brush, then permanently mounted with a methacrylate copolymer, and covered with a glass cover slip (Flo-Texx liquid cover slip, Lerner Lab.).

For the visual method, scale circuli were counted twice by the same reader, along a central radius from the focus to the edge, on the anterior side, at 125× magnification on an Olympus BH-2 microscope. If counts were not the same, they were counted a third time. Only 1 out of 45 required a third count, and for that scale the counts that were the same were used for comparison with automated computer counts.

For automated counting, scales were digitized using the same magnification and radius as visual counts. Scale images were detected by a Ikigami ITC-510 video camera (625-line resolution) mounted on the microscope, digitized by a Matrox PIP-512B image analyzer, and stored in computer memory in a matrix of 512 × 512 picture elements (pixels) with 256 gray levels for each pixel. A PC-AT 286 computer with a 10-meg Hz processor, 1-meg RAM, and math coprocessor controlled the image analyzer. A 40-megabyte hard disk and a floppy disk drive were used for image and data storage.

Once the image was digitized, it was displayed on a Panasonic PM 205A video monitor (1000-line resolution) and a mouse was used to control the movement of a cursor mark projected on the image. The cursor was then positioned to select two points defining a transect from the focus to the edge of the scale perpendicular to the circuli (Fig. 1). Light intensities (gray levels) of three transects, each one pixel apart and one pixel wide, were simultaneously stored to the hard disk. Each transect was then analyzed using a Fortran program to identify and count scale circuli. The algorithm applied a moving average (7, 8, 9, and 10 pixel averages were tried) to smooth each transect and then searched for local minima (e.g., 10 pixels on either side of the inflection point corresponds to a local minimum within a search width of 20 pixels; search widths of 18, 20, 22, and 24 pixels were tried). The Fortran counting algorithm compared adjacent pixels and determined if light intensity increased or decreased. Subsequently, an increment was counted only after the following two criteria were satisfied: (1) an inflection point was detected, i.e., a change in light intensity from decreasing to increasing, and (2) the inflection point was the minimum light intensity within the specified search width. Depending on the scale size, one to five images were needed to complete a scale count (i.e., with smaller scales the complete scale was included in the digitized image, but with larger scales several images were needed at the same magnification to include all circuli from the focus to the edge). The computer counts (aver-

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**Figure 1**
Photograph of a weakfish scale with 29 circuli (29 circuli + edge = count of 30). Arrow depicts counting transect from focus to perimeter along the anterior growing side (transect line = 0.5 mm).

ages of the three counts from individual scales) were then regressed against the visual counts.

## Results and discussion

Application of a nine-pixel smoothing interval on the transect data combined with a 20-pixel local-minima search width, produced the highest coefficient of determination ($r^2$ 0.99) between the automated and visual counts (Fig. 2). Other combinations of smoothing interval and search width resulted in lower coefficients. The present program allows adjustment of smoothing interval and search width to optimize its use with other fish species. Computer counting was approximately 3.3 times faster than visual counting. The visual method showed a slightly higher precision compared with computer counting, but savings in time more than compensates for this small increase in error (Table 1). In addition, the concentration needed and subsequent fatigue in visual counting compared with computer counting are difficult to measure, yet computer counting was considered much easier by all scale readers.

Microcomputer systems that can digitize increments from scales, otoliths, and other bony structures have been previously reported and demonstrated potential for automated counting (McGowan et al. 1987). The present system makes an advance over other systems by using the local-minimum method of increment identification. Previous methods usually use threshold-light intensity levels to identify increments that may produce discrepancies between computer

**Table 1**
Comparison of counts and counting times of scale circuli from weakfish *Cynoscion regalis* between computer and visual methods from a random subsample of those counted. Each scale was from a different fish.

| | Visual counts | | | | Computer counts | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Scale | 1st | 2d | 3d | Time (s) | 1st | 2d | 3d | $\bar{x}$ | Time (s) |
| 1 | 36 | 36 | | 46 | 38 | 38 | 38 | 38.0 | 13 |
| 2 | 32 | 32 | | 42 | 31 | 31 | 32 | 31.3 | 16 |
| 3 | 32 | 32 | | 41 | 31 | 32 | 33 | 32.0 | 13 |
| 4 | 37 | 37 | | 46 | 39 | 38 | 38 | 38.3 | 12 |
| 5 | 32 | 32 | | 42 | 31 | 31 | 32 | 31.3 | 16 |
| 6 | 30 | 30 | | 39 | 30 | 30 | 30 | 30.0 | 12 |
| 7 | 50 | 51 | 50 | 106 | 51 | 52 | 50 | 51.0 | 13 |
| 8 | 60 | 60 | | 82 | 64 | 62 | 61 | 62.3 | 35 |
| 9 | 46 | 46 | | 51 | 48 | 47 | 49 | 48.0 | 19 |
| 10 | 43 | 43 | | 45 | 44 | 44 | 44 | 44.0 | 15 |
| 11 | 58 | 58 | | 94 | 60 | 60 | 60 | 60.0 | 26 |
| 12 | 64 | 64 | | 74 | 66 | 67 | 65 | 66.0 | 25 |
| 13 | 60 | 60 | | 80 | 61 | 58 | 61 | 60.0 | 31 |
| 14 | 49 | 49 | | 56 | 50 | 50 | 50 | 50.0 | 15 |
| 15 | 58 | 58 | | 69 | 60 | 58 | 58 | 58.7 | 14 |
| | | | | $\bar{x}$ 60.9 | | | | | $\bar{x}$ 18.3 |
| | | | | SD 21.7 | | | | | SD 7.4 |

Paired $t$-statistic = 8.85, $t$ critical value (level = 0.05) = 2.145, therefore there is a significant difference between counting time.

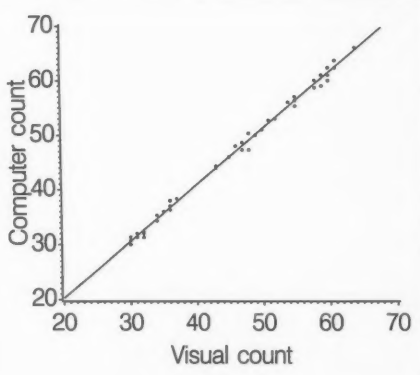


**Figure 2**
Linear regression of computer automated count on visual count of scale circuli from weakfish, *Cynoscion regalis* ($N$ 45 fish, $r^2$ 0.99, $y = 1.03x - 0.3$).

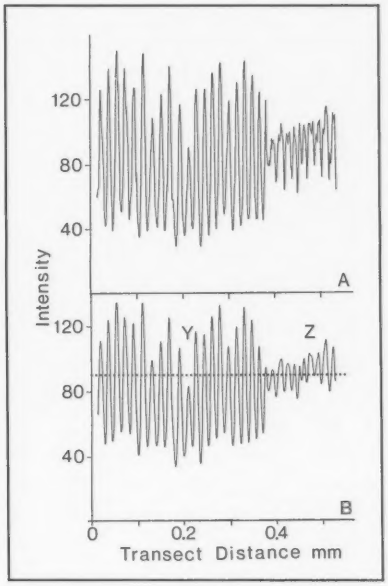


**Figure 3**
Light intensities along a transect taken from a single scale by distance in mm. (A) Light intensities of a single transect. (B) Smoothed data using a nine-point moving average. Dashed line represents a threshold light intensity of 90. Lowering the threshold to include peak Y would eliminate peaks under Z.

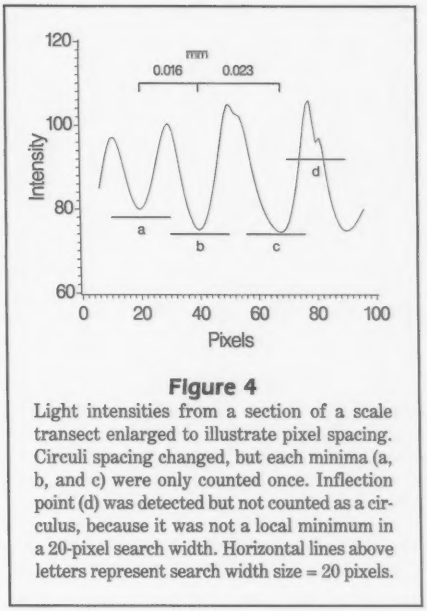


**Figure 4**
Light intensities from a section of a scale transect enlarged to illustrate pixel spacing. Circuli spacing changed, but each minima (a, b, and c) were only counted once. Inflection point (d) was detected but not counted as a circulus, because it was not a local minimum in a 20-pixel search width. Horizontal lines above letters represent search width size = 20 pixels.

and visual counts, because background intensity levels change as the transect moves across the otolith or scale. Thus, some areas may be counted incorrectly when they fall below the selected threshold level as shown for a transect across a weakfish scale (Fig. 3). The local-minimum method solves this problem, since identification of increments is only dependent on adjacent pixel-light intensity levels. The local-minimum method also responds to changes in increment spacing: as increment spacing increases (measurements from one typical scale ranged from 10.3 to 22.9 $m^{-6}$) the algorithm moves greater distances (more pixels) along the transect, but does not count more increments until another minimum is detected. For example, in Figure 4, increments a, b, and c were each counted as one circulus despite changes in circuli spacing, but inflection point d was not counted because it was not a local minimum within a 20-pixel search width.

Increments narrower than the selected search width would cause errors (e.g., microincrement spacing width = 10 pixels, but search width = 20 pixels). However, this problem can be corrected in three ways: (1) reduce the search width; (2) increase the magnification of the scale or otolith, e.g., from 125 to 400; or (3) increase the number of pixels between increments, i.e., increase the resolution of your system as discussed below. In addition, the true limit of counting narrow increments is not the algorithm, but the resolution limit of the light microscope. After projection of the image onto the video monitor, one pixel corresponds to an actual distance of about 0.2 $m^{-6}$ (with the light microscope at 1000×). This 0.2 $m^{-6}$ size is the maximum theoretical resolution of any light microscope (Eastman Kodak Co. 1980). In addition, "...the functional limits are invariably higher than those derived theoretically" (Campana et al. 1987), therefore several pixels may be present even between the smallest detectable increments. Other advantages of the present system, as well as other systems, include elimination of data entry and associated transcriptional errors, and establishment of repeatable criteria for ageing of fishes.

A disadvantage of the present system and other similar systems is that clearly defined increments are needed. This was not a problem with weakfish scales because circuli are distinct (Fig. 1), but application to otolith increments may need further refinement. Another disadvantage is that most systems need multiple images to complete a transect reading of a single scale or otolith, which may increase processing time and errors. The multiple-image-per-transect problem results from a limiting number of pixels (512 × 512 pixels) in our digitizer, such that lower magnifications (25 or 40) that would encompass the entire transect do not contain enough pixels for accurate identification of increments. Systems with greater pixel resolution (e.g., 1024 × 1024) would alleviate this problem, and are now commercially available.

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